THE *DIOSPYROS SALICIFOLIA* COMPLEX (EBENACEAE) IN MESOAMERICA

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ABSTRACT

The taxonomy of the *Diospyros salicifolia* complex was examined using traditional taxonomic methods and multivariate statistics. Seven species are currently known in Mesoamerica. *Diospyros acapulcensis* Kunth, which occurs from Panama to Jalisco and Veracruz, Mexico, is separable into nine subspecies. *Diospyros aequoris* Standl., a plant of western Mexico from Sinaloa to Oaxaca, is separable into six subspecies. *Diospyros salicifolia* Humb. & Bonpl. ex Willd. is endemic to the Acapulco region of Guerrero, Mexico, and may be of recent hybrid origin. *Diospyros yucatanensis* Lundell, occurring in the Yucatan Peninsula and nearby regions of Mexico and Central America, is separable into two subspecies. *Diospyros intricata* (A. Gray) Standl. is currently known only from the Cape region of Baja California Sur, Mexico. As circumscribed here, interspecific hybridization is thought to be rare in the complex, but intermediates between subspecies sometimes form at the edges of their ranges. Panamanian specimens of putative *D. inconstans* Jacq., belong to this complex, and the recently described *D. amanap* B. Walln., seems to as well. Descriptions are provided for *D. salicifolia, D. acapulcensis, D. aequoris* and *D. yucatanensis*, and within these species nine new subspecies are described, and five new combinations are made. A key to the taxa is provided, along with distribution maps, illustrations and photos of types and living material.

RESUMEN

Se examinó la taxonomía del complejo *Diospyros salicifolia* mediante métodos taxonómicos clásicos y análisis multivariantes. Se conocen normalmente siete especies en Mesoamérica. *Diospyros acapulcensis* Kunth, que se extiende desde Panamá a Jalisco y Veracruz, México, se puede separar en nueve subespecies. *Diospyros aequoris* Standl., una planta del oeste de México que va de Sinaloa a Oaxaca, es separable en seis subespecies. *Diospyros salicifolia* Humb. & Bonpl. ex Willd. es endémica de la región de Acapulco en Guerrero, México, y puede ser de reciente origen híbrido. *Diospyros yucatanensis* Lundell, de la Península de Yucatán y regiones próximas de México y América Central, se puede separar en dos subespecies. *Diospyros intricata* (A. Gray) Standl. se conoce sólo de la región del Cabo de Baja California Sur, México. Tal como están circunscritos aquí, la hibridación interespecífica se piensa que es rara en el complejo, pero a veces se forman intermedios entre subespecies en los extremos de su rango. Especimenes panameños del putativo *D. inconstans* Jacq., pertenece a este complejo, y el recientemente descrito *D. amanap* B. Walln., parece que también. Se aportan descripciones de *D. salicifolia, D. acapulcensis, D. aequoris* y *D. yucatanensis*, y en estas especies se describen nueve nuevas subespecies, y se hacen cinco nuevas combinaciones. Se aporta una clave de los taxa, junto con mapas de distribución, ilustraciones y fotos de los tipos, y de material vivo.

INTRODUCTION

As part of a revision of *Diospyros* for Mexico, a study of the *D. salicifolia* complex was conducted in order to address taxonomic inconsistencies in the literature. We used a combination of conventional taxonomic methods, multivariate statistics and extensive fieldwork in Mexico, in order to resolve uncertainty regarding the proper application of names, assess taxonomic boundaries, emend species descriptions, and construct a useable key for the taxa. Early workers described a number of 3–4-sepalous *Diospyros* in Mesoamerica that seem to form a natural group that we refer to as the *Diospyros salicifolia* complex. Morphometrics, including

multivariate statistics, were used to explore continuous variation and the utility of quantitative vegetative and reproductive characters in the circumscription of taxa throughout the distribution of the complex in Mesoamerica.

***Diospyros salicifolia* complex:** female flowers solitary, rarely in a 3-flowered cyme with two flowers aborting, or a single female flower terminating an otherwise male inflorescence; calyx lobes 3–4, accrescent (mostly widening, but lengthening markedly in *D. yucatanensis* subsp. *spectabilis*); female flowering calyx mitriform, sometimes tearing or dehiscing at the sinus as the fruit and/or calyx enlarges; styles 3, varying from a fully fused column to free to the base, minutely hairy, stigmas bifid, corolla tube sericeous with 3–4 glabrous zones around the base; fruits with three pairs of locules (these pairs difficult to see in mature fruit, but conspicuous during dissection of immature ovaries), the members of a given pair divided by an apparently complete septum; fruit wall indehiscenct to vaguely or (infrequently) conspicuously dehiscent; flesh ± clear and gelatinous, but becoming reddish, translucent and vitreous when dry; leaves usually evenly distributed along the stem; hairs throughout the plant with fluid-filled lumens, the fluid clear in life, but usually turning reddish upon drying (essentially non-capitate simple glandular hairs–some plants also with occasional non-capitate multi-branched glandular hairs); seeds reddish, especially in life, distributed by birds (White 1978, pers. obs.) and mammals, probably carnivores (pers. obs.).

There are two Mesoamerican *Diospyros* species complexes that could be confused with the *salicifolia* complex.

***Diospyros tetrasperma* complex:** Female flowers usually solitary; calyx lobes 4–5, not markedly accrescent; female flowering calyx not mitriform; interior of the fruiting calyx often ridged and hairy in the upper tube and basal lobe, sinus indehiscent/not tearing; styles 2 pairs or 1 with 5 branches, stigmas 4–5; fruits 4–5 loculed, the locules all divided by a seemingly complete septum; the flesh of the fruit ± gelatinous (rarely fleshy), becoming reddish, translucent and vitreous when dry; leaves sometimes crowded at the ends of stems on short shoots. Members include *D. tetrasperma* Sw., *D. anisandra* S.F. Blake, *D. johnstoniana* Standl. & Steyerm., *D. bumelioides* Standl., and *D. yatesiana* Standl. ex Lundell.

***Diospyros campechiana* complex:** Female inflorescence 1–4-flowered; calyx lobes 4–5, not markedly accrescent; female flowers not mitriform; fruiting calyx weakly attached to the fruit, tending to persist on the pedicel rather than the fruit, the tube spreading and lobes patent to reflexed; style 1 with 2 branches; fruits 1–4-loculed; the amount of flesh present relatively meager by comparison to members of other complexes, reddish, translucent and vitreous when dry (probably clear and gelatinous in life); the hairs minute, and include dark red to nearly black, slightly flexuose to straight, appressed (or nearly so) hairs; seeds few, loosely contained in the fruit of herbarium specimens; leaves medium to large, not crowded on the ends of the shoots, the petioles sometimes with transverse fissures. Members include *D. campechiana* Lundell, *D. hartmanniana* S. Knapp, and *D. panamense* S. Knapp.

Members of the *salicifolia* complex were formerly treated as members of the genus *Maba* J.R. Forst. & G. Forst. (e.g., Hiern 1873) or *Macreightia* A. DC. (e.g., De Candolle 1844). Herbarium specimens often have been identified using Standley's treatment of the group under the genus *Maba* (1924), but typically bear the appropriate combination in *Diospyros* following Standley (1935). Interestingly, no specimens determined as *D. portus* Standl. (= *Maba rekoi* Standl.) were seen during this study, although this little-known taxon appeared in Standley's treatment. Specimens from the Yucatan Peninsula and northern Guatemala are usually identified as *D. yucatanensis* or *D. spectabilis* following Lundell (1937, 1942).

Several workers, such as B. Wallnöfer, C. Whitefoord and S. Knapp, and F. White, ascribe Mesoamerican material of this complex (with the exception of the Baja California endemic *D. intricata*, and *D. amanap* and *D.* aff. *inconstans* from Panama) to *D. salicifolia* Humb. & Bonpl. ex Willd., sometimes with the postscript 'sensu lato.' The different opinions concerning the taxonomic boundaries within this highly variable complex, and the trends seen in the identification of material, are related to the application of three names, *D. acapulcensis* Kunth, *D. salicifolia* Humb. & Bonpl. ex Willd., and *D. albens* Presl. These names are all based

on collections from the Acapulco region of Guerrero held in historical European collections at Paris (P), Willdenow (B-W), and Vienna (W) respectively.

TYPE MATERIAL FROM GUERRERO, MEXICO

The name *Diospyros salicifolia*, published by Willdenow in 1806, is based on material ("*Humboldt & Bonpland s.n.*") collected in the Acapulco region of Guerrero, Mexico, and is the oldest name in the complex. Unfortunately, the holotype at Berlin (B-W19250-01) consists only of a branchlet with some very immature leaves, one disconnected mature leaf, and one disconnected fruit (Fig. 1). In preparation of Flora Veracruz, Pacheco (1981) had doubts about the application of the name *D. salicifolia* because the type material is insufficient, and thus used the name *D. veraecrucis* Standl. for plants growing on the east coast of Mexico. However, she mentioned Frank White's suggestion that *D. salicifolia* is the correct name for the species in Veracruz. Whitefoord and Knapp (1998-onward) commented that the type specimen of *D. salicifolia* is "depauperate," but concluded that material they attributed to *D. salicifolia* in southern Mexico and Central America was in agreement with the holotype of *D. salicifolia* based on microfiche ("microficha BM! ex B-W"). Recently, the Botanic Garden and Botanical Museum Berlin-Dahlem has made it possible to view on the Internet a high quality image of the type specimen of *D. salicifolia* held in the Willdenow Herbarium (B-W), including the informative abaxial surface of the mature leaf.

The name *D. acapulcensis* was published in 1818 by Kunth, who worked on the collections of Humboldt and Bonpland in the herbarium at Paris between 1815 and 1828 (Hiepko 1987). The type (Fig. 2a–b) is a specimen in the Paris Muséum National d'Histoire Naturelle (P), unfortunately bearing roughly the same scanty label data as the type of *D. salicifolia* at Berlin, "*Humboldt & Bonpland s.n.*" The locality indicated on the preprinted label is "Amérique Équatoriale." The determination of the specimen as "*Diospyros acapulcensis*" is in the handwriting of Kunth. Because of the general similarity of these two species and the inadequacies of the type specimens, this collection was considered an isotype of *D. salicifolia* by Wallnöfer (by annotation c. 2002) and Whitefoord and Knapp (1998-onward). Wallnöfer also annotated this specimen as the lectotype of *D. acapulcensis* in 2002. As far as we can tell, this lectotypification was not formally published.

The confusion of *D. acapulcensis* and *D. salicifolia* is long standing. In the earliest treatment of the genus to include members of the *salicifolia* complex, Alphonse De Candolle (1844) included *D. salicifolia* in his concept of *Macreightia acapulcensis* (Kunth) A. DC. with a question mark. But, in his monograph of the Ebenaceae, Hiern (1873) stated that "the foliage is sufficiently different" between *D. salicifolia* (= *Maba salicifolia* Hiern) and *D. acapulcensis* (= *Maba acapulcensis* Hiern) for them to be treated as separate species. However, it is unclear to us what material he actually compared, since in reference to *Maba salicifolia*, he cites having seen only "*Humboldt and Bonpland*" from "Equatorial America," which would seem to refer to the type collection of *D. acapulcensis* in Paris. However, this citation seems dubious, since his description of *D. salicifolia* is more consistent with the type at Berlin (*D. salicifolia*) than the type at Paris (*D. acapulcensis*), and lacks a description of the dissected seed mounted on the Paris specimen. We are further troubled by the absence of the *Humboldt and Bonpland* specimen from the enumeration of specimens in Hiern's monograph. Hiern indicates in the introduction to his monograph that he examined the type material in the Willdenow collection at Berlin. It would be astonishing if he had not made use of the type collection of *D. salicifolia*. In reference to *D. acapulcensis*, Hiern cites a single specimen, with the locality data "Mexico, Acapulco, *Bonpland*," which is consistent with label data on a sheet at Paris (P-271690) identified as *D. acapulcensis*, but not currently available to us. Standley (1924) treated *D. salicifolia* and *D. acapulcensis* (under the genus *Maba*) as separate species. In his key he separated them based on differences in leaf shape at the apex and lamina vestiture. He considered material from Acapulco referable to *D. salicifolia*, but did not expand on the distribution of *D. acapulcensis*, other than to state that the type was from Acapulco. The status of these species was still not completely clear.

More recently, *D. salicifolia* and *D. acapulcensis* have been treated as synonyms, apparently beginning with a broad concept of *D. salicifolia* by F. White, but also based on the fact that the two type collections

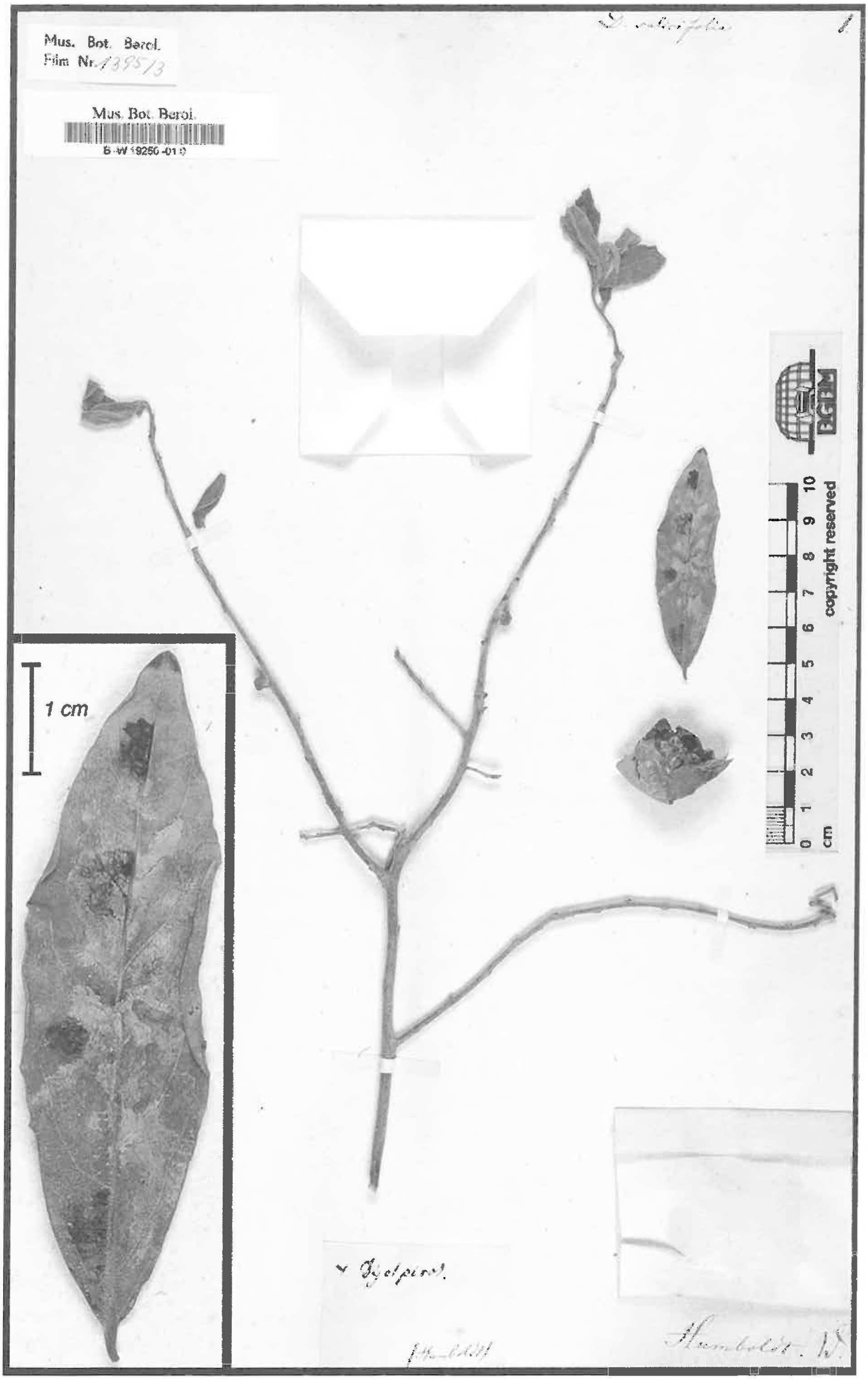

Fig. 1. Photo (Röpert, D) of *Humboldt & Bonpland s.n.* (B-W-19250-01), the holotype of *Diospyros salicifolia* Humb. & Bonpl. ex Willd., with (inset) detail of abaxial leaf surface.

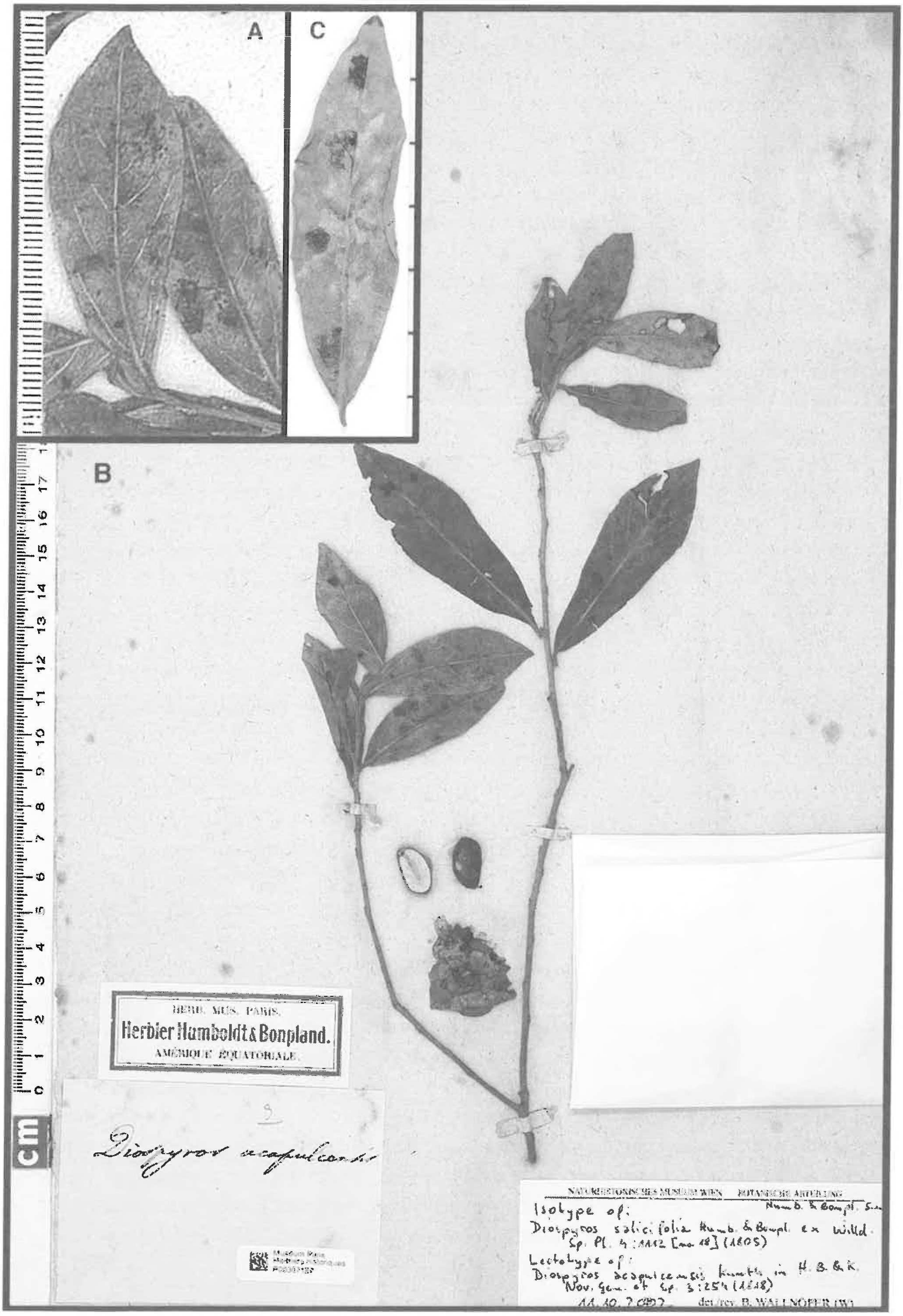

Fig. 2. A–B. Photo (Museum National d'Histoire Naturelle-Paris) of *Humboldt & Bonpland s.n.* (P-307187), the lectotype of *Diospyros acapulcensis* Kunth. A. Abaxial leaf surface. B. The annotated specimen. C. Abaxial leaf surface of *Diospyros salicifolia* Humb. & Bonpl. ex Willd., from *Humboldt & Bonpland s.n.* (B-W-19250-01).

(B-W-19250-01 and P-307187) have been considered duplicates by some workers. However, the type specimen of *D. salicifolia* (*Humboldt & Bonpland s.n.*) in the Willdenow collection (B-W-19250-01) does not represent the same species as the type of *D. acapulcensis* at the Paris Muséum National d'Histoire Naturelle (P-307187.) These two specimens have therefore been erroneously considered duplicates. The B-W specimen (Figs. 1, 2c) represents *D. salicifolia*, a taxon that is evidently endemic to coastal regions around Acapulco, Guerrero including Isla Roqueta in Acapulco Bay. This species has been collected at Acapulco on a number of occasions in recent times, but nowhere else. The Paris specimen of *Humboldt & Bonpland s.n.* (Fig. 2a–b) represents *Diospyros acapulcensis* (P-307187, designated below as the lectotype). This taxon occurs through much of western Mexico, and while it does occur near Acapulco, in the state of Guerrero it is more common inland in the municipalities of Chilpancingo, Achotla, and Iguala. The closest collections to Acapulco that we have seen are from about 15 km away at 200 m elevation near Rio Papagayo (Fig. 3).

These two specimens also cannot be part of the same gathering because they are in different phenological stages: both specimens have fruit, but the Berlin specimen (*D. salicifolia*) is almost entirely without leaves except for very immature ones at the shoot apices. It represents a collection from the beginning of the growing season, from a plant that had a few old persisting leaves from the previous growing season. The single mature leaf on the collection is elliptical with a base that is rounded to the petiole. The Paris specimen (*D. acapulcensis*) represents a plant from a later phenological stage, as it still has numerous mature leaves, and is without immature leaves at the apex. The laminas on the Paris specimen are all oblanceolate to obovate, and have a cuneate to slightly rounded base. When the abaxial leaf surfaces of the specimens are closely compared (Fig. 2a, c) additional differences are readily apparent. The lateral veins of the Paris specimen are thick and straight and diverge at an acute angle, while those in the specimen at Berlin are finer and diverge at a greater angle, gradually curving toward the leaf apex. The Paris specimen probably came from near Acapulco, but from a slightly more interior location than the Berlin specimen. It is unclear to us what facts Kunth had that indicated the Paris collection was made in a littoral zone, which seems a more likely habitat for *D. salicifolia*. This information may have come from one of the other Paris specimens (currently unavailable to us), in which case, that specimen should be evaluated carefully to see if it is *D. salicifolia*. Other possibilities include miscorrelation of field notes (unknown to us) attributable to *D. salicifolia* collections, or use of the term "littoral" in a very broad sense. There are two other specimens at Paris identified as *D. acapulcensis* that are currently unavailable, but which seem to have label data similar to the chosen (below) lectotype: *Bonpland* s.n. (P-271689) from "Mexico," and *Bonpland* s.n. (P-271690) from "Acapulco, Mexico." The specimen annotated by Wallnöfer as lectotype (P-307187) is consistent with the original description of *D. acapulcensis*. This description gives a rather complete account of seed anatomy, which is consistent with the carefully mounted dissected seed on the specimen favored by Wallnöfer. We believe that P-307187 was important in the initial description of *D. acapulcensis*, and below we formally designate it as the lectotype.

The other species involved in this nomenclatural issue, *Diospyros albens* C. Presl, was described in 1835 from material collected by T. Haenke at Acapulco in about 1791 (although the collection is undated). Based on a photograph of the type (*Haenke s.n.*, W-31942) obtained from Field Museum, the specimen appears to be a collection of *D. salicifolia* with male flowers and young leaves. We cannot separate this material from other specimens of *D. salicifolia* with young leaves (e.g., *W. Boege 452*), and the two names are here treated as synonyms. The name *D. albens* appears occasionally in the literature and sometimes on herbarium specimens. For instance, Standley (1924) seems to have used this name in reference to *D. aequoris* subsp. *tehuantepecensis*, a subspecies proposed here for the state of Oaxaca, and later in reference to the nominate subsp. of *Diospyros yucatanensis* (Standley 1930).

METHODS

Taxonomic Methods.—All of the relevant literature, loaned specimens, including types, and images of types, that could be obtained were evaluated. Additionally, numerous specimens attributable to the *salicifolia* com-

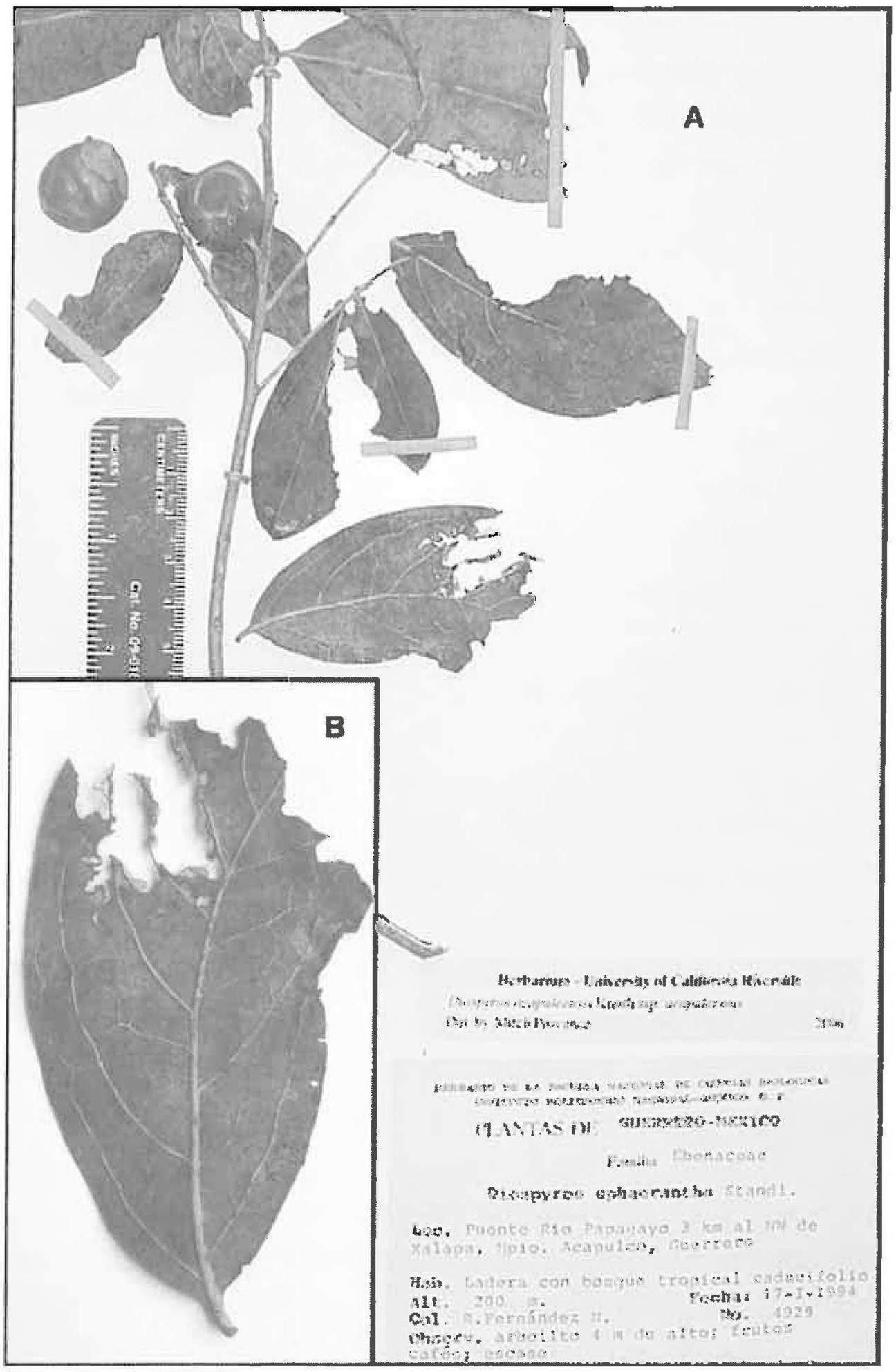

Fig. 3. *Diospyros acapulcensis* subsp. *acapulcensis* from Puente Rio Papagayo, Guerrero (*R. Fernandez N. 4929,* IEB). A. Fruiting branchlet. B. Abaxial leaf surface.

plex were collected by the authors in the states of Baja California Sur, Sinaloa, Nayarit, Jalisco, Michoacan, Guerrero, Campeche, and Oaxaca, Mexico and the Nicoya Peninsula, Costa Rica. We have studied about 900 specimens referable to this complex.

We generally agree with de Queiroz (1998, 2007) that species can be thought of as "separately evolving metapopulation lineages," where lineage refers to an "ancestor-descendant series," and metapopulation refers to "an inclusive population made up of several lineages" (de Queiroz 2007) and appreciate his eclectic approach to acceptable lines of evidence that can be used in assessing lineage separation. However, we remain uncomfortable with the practical implications of this general approach for the working systematist, especially given the ambiguities of lineages composing metapopulations, the temporal segments of which in turn compose the other lineages called species, and feel that the "general lineage concept" is not yet operational.

Our approach is been based on examination of morphological variation observed in a sample of specimens preserved in herbaria of the world over the past 200+ years, and in living material encountered (and photographed) during field studies in Mexico and Costa Rica. Collections were sorted into groups based on

morphological characters, and secondarily based on geography. We believe that useful taxonomic groups should have unique and generally coherent geographical distributions. Groups identified in our preliminary sorting were considered taxonomic hypotheses warranting continued investigation. Comparisons were made between specimens assigned to each group, and between those specimens and type specimens. We also examined specimens in light of type descriptions, existing floristic and monographic treatments, and the annotations of previous workers. Published names applicable to the identified groups were determined, and the names having priority were determined for each group. Emended descriptions were constructed for species based on studied herbarium specimens and field observations.

De Queiroz does not discuss the use of subspecies or other infraspecific ranks, though these have been widely used by taxonomists, and even though such ranks appear quite appropriate for populations in his zone of lineage separation (de Queiroz 2007, fig. 1) where only some of the properties of species have been acquired. This is the way that infraspecific ranks have traditionally been used by biologists. Here we use the subspecific rank, perhaps in a way similar to other recent workers (e.g., Mulcahy 2007), to communicate our hypothesis of an incipient species within a metapopulation, although in some cases this may represent formerly separate species in the process of merger due to secondary contact resulting from migration and/or environmental change. We are reluctant to describe populations as full species when it appears that botanical exploration between these populations has been inadequate and where the morphological differences separating them are not great. Further exploration could reveal populations with mixtures of the defining characteristics of the two initial populations. Although it is certain that at least some of our subspecies would be treated as full species under concepts treating diagnosable terminal taxa in a cladogram as species (e.g., Mishler & Theriot 2000), we have taken a conservative course in treating them as subspecies. Future studies may reveal that some of our subspecies have diverged more than we can now see and that they are best treated as full species. In any event, we feel it is most important to call attention to these entities. Their taxonomic status can always be changed later, but only if the taxa are first described so that other biologists know they exist.

In accordance with this approach, the material assigned to each species was examined so that consistent differences in morphology, correlated with contiguous geographic areas could be detected. If morphological differences between subgroups within a species proved to be predictive of geography, and the subgroup distributions were allopatric or parapatric, then recognition at subspecific rank was strongly considered. We consider subspecies to be geographic races marked by one or more morphological features, not random variants that appear throughout the distribution of a species. There should be a genetic basis for the morphological variation observed between subspecies, although it is understood that differences in environmental distribution complicate efforts to tease genetic effects apart from environmental influences, especially in baseline taxonomic studies that may have few representatives for certain taxa. In an effort to minimize the influence of environmental factors on our subspecies delimitation, we conducted analyses of covariance using elevation (a proxy for variation in the environment) as a cross effect on leaf and inflorescence traits between subspecies. These analyses (to be presented in a later paper) suggest that quantitative variation in many of these traits is likely to have a genetic component. Furthermore, they highlight an interaction between genetic and environmental factors for some of these traits. In other words, some characters varied inversely with elevation for different subspecies. For instance, the venation parameter leaf width : distance between lateral veins, decreased with elevation for *D. acapulcensis* ssp. *guanacastensis*, while it increased with elevation for *D. acapulcensis* ssp. *rivensis*.

We expect subspecies to hybridize with other subspecies, and if we found that two occupying the same range and habitat did not hybridize with one another, we would propose that they be treated as separate species. But, we do not necessarily expect reproductive barriers to be complete between plant species, although we expect them to be greater than between subspecies.

We carefully studied the floral anatomy of each taxon we could, but descriptions of internal floral structures are still sometimes based on relatively few observations, and the floral anatomy of all taxa needs

more study. In this treatment we use 'lanceolate' in the sense of Jackson (1916), being broadest near the lower third of the leaf, not at mid-leaf in the sense of Stearn (2000).

For new combinations, at least one specimen is cited for each relatively small political unit of occurrence (e.g., municipality, department). Most material examined is cited for new subspecies. Collections of interspecific hybrids and subspecific intermediates are cited in Appendix 1. Descriptions apply to herbarium material except when indicated, or when obviously referring to fresh material. Comments on ecology and ethnobotany are based on specimen label data, published field notes, vegetation maps, and personal observations. Map coordinates geo-referenced by the authors are given in brackets. Distribution maps were constructed using The Generic Mapping Tools 4.1.4 (Wessel & Smith 2006) accessed through OMC (Weinelt 2006) and amended using Adobe Photoshop (Ver. CS 8.0, Adobe Systems Incorporated, San Jose, CA). Photographs and illustrations are by the first author unless specified otherwise.

Statistics Methods.—The dataset used in the multivariate statistics consisted of 360 fruiting collections of Mesoamerican *Diospyros* referable to the *salicifolia* complex (a list of accessions is available from the first author). Leaf measurements were based on an average of the three largest leaves, except (rarely) when only two acceptable leaves were present and the specimen was considered especially important for inclusion. The statistical software used was JMP Statistical Discovery (Ver. 6.0, Macintosh Version, SAS Institute Inc., Cary, NC).

Prior to principal component analysis (PCA), strongly correlated characters were identified and eliminated. Since exclusion values are somewhat arbitrary, two such values ($R < 0.7$, $R < 0.8$) were explored. When a correlation was above the exclusion value, one character was retained with preference given to leaf length or leaf width, and lengths over ratios. Leaf length and width were highly correlated. Instead of choosing arbitrarily which of the fundamental lamina measurements should be excluded, we decided to retain two character sets at each exclusion value (i.e., one set with width excluded, the other with length excluded). PCA was used on each of the four sets to discern the relative separation of species groups in multidimensional subspace, and to identify the quantitative variables explaining the most variation in the data. PC scores were scaled to unit variance, thus grouping is discerned from 'GH biplots.' Where the first three components returned eigenvalues greater than one (e.g., many components were needed to explain the observed variation), a varimax factor rotation was performed using all of the components having eigenvalues of one or more in order to make the results interpretable.

TAXONOMIC TREATMENT

The majority of South American *Diospyros* specimens were unavailable for this study, and consequently the distribution of the *salicifolia* complex in South America could not be addressed. Whitefoord and Knapp (1998-onward) reported "*D. salicifolia*" for Columbia, but they did not cite a specimen. We have not seen a specimen of *D. salicifolia* sensu lato from South America, but we do not doubt the presence of *D. acapulcensis* in Columbia. The dearth of available South American specimens also meant that the taxonomic status of *D. inconstans* Jacq. in Mesoamerica could not be addressed completely. All putative Mesoamerican *D. inconstans* specimens we examined were collected in Darien Province, Panama. This material is uniform and we believe it represents a single species perhaps related to, but nonetheless different from, those species represented by the smattering of collections we received from South America and the Caribbean. In our opinion the South American specimens determined by other workers as *D. inconstans* represent more than one taxon. The leaves of the Panamanian material seem consistent with an image seen online (Tropicos.org 2008) of a sterile collection from Columbia (*Bertero s.n.* [MO-1905992]) annotated by B. Wallnöfer as an " "isotype" of: *Diospyros berterii* ... = *D. inconstans* s. lat. Jacq." At any rate, the Panamanian collections cited here in Appendix 2 as *D.* aff. *inconstans* are clearly attributable to the *salicifolia* complex, most obviously because of the male flowers in 2–3-flowered cymes, solitary female flowers, the trimerous calyx which is clearly mitriform in the flowers of both sexes, and the overall appearance of the fruiting calyx and mature fruit.

Wallnöfer (2005) recently described a new species, *D. amanap* B. Walln., based on one collection from

Columbia and another from Darien Province, Panama. Although we have not had the opportunity to compare our material with these collections, we think it is unlikely that the *D.* aff. *inconstans* specimens cited here represent *D. amanap*, as they are not in accord with the species description and because Wallnöfer annotated one of the specimens we studied as *D. inconstans* sensu lato. Unfortunately, Wallnöfer did not provide an illustration or photograph of *D. amanap*, or make any comparisons of *D. amanap* to other taxa. The species is described as having a trimerous accrescent calyx and probably a 6-locular fruit (Wallnöfer 2005), and is therefore likely to belong in the *salicifolia* complex.

KEY TO THE MESOAMERICAN SPECIES OF THE *DIOSPYROS SALICIFOLIA* COMPLEX (EXCLUDING *D.* AFF. *INCONSTANS* AND *D. AMANAP*)

1. Petioles < 2 mm long; lamina 10–30(–40) mm long, 5–17 mm wide, obovate, rounded apically, the base cuneate, sparsely to moderately hairy below (densely puberulent when young), the hairs straight, appressed; fruiting calyx small (calyx length + lobe width 12–16 mm); shrubs, mostly < 2.5 m tall; Cape Region of Baja California Sur, including Isla Cerralvo ____ **D. intricata**
1. Petioles > 2 mm long; lamina 18–155 mm long, 11–65 mm wide, shape variable, density of abaxial vestiture, and shape of abaxial hairs variable; fruiting calyx larger (calyx length + lobe width usually (15–)17–25(–32) mm; trees or shrubs, 1–28 m tall; not known from Baja California.
   2. Lamina chartaceous to subcoriaceous, 18–110 mm long, usually elliptic, oblong, oval or nearly circular, the base rounded to subcordate, often coarsely wrinkled above; W Mexico.
      3. Flowering female calyx tube 1.2–1.8 mm long; lamina mostly 60–110 mm long, length : width = 2.2–4.2 : 1; base more narrowly rounded than in *D. aequoris* (length : width at 0.25 = 3.3–4.8 : 1); apex rounded (length : width at 0.75 = 3–4 : 1), lamina not wrinkled above, glabrate to sparsely hairy when mature; 3° venation inconspicuous below, faintly raised or not apparent above; currently known only from the immediate vicinity of Acapulco, Guerrero, < 200 m ____ **D. salicifolia**
      3. Flowering female calyx tube 2.3–6 mm long (1.5 mm long in one subsp. from interior Oaxaca); lamina 18–81 mm long, length : width = 1.1–2.8 : 1; base rounded to subcordate (length : width at 0.25 = 1.5–4.3 : 1); apex rounded to acute (length : width at 0.75 = 1.3–3.5 : 1), lamina often wrinkled above, moderately to densely pubescent below when mature; 3° venation usually prominent below and impressed above; widespread in W Mexico, < 1200 m ____ **D. aequoris**
   2. Lamina membranaceous to chartaceous, rarely subcoriaceous, 45–160 mm long, lanceolate to ovate, or oblanceolate to obovate, sometimes elliptic, oblong or oval, the base rounded, attenuate, or cuneate, decurrent on the petiole, sometimes abruptly, not coarsely wrinkled above; Jalisco, Mexico to Panama.
      4. Flowering female calyx tube 1.2–1.8 mm long; lower lamina surface glabrate to sparsely hairy when mature (moderately hairy when immature), the hairs appressed to subappressed, straight, or nearly so, without swollen remnant hair bases conferring a papillose appearance; currently known only from the immediate vicinity of Acapulco, Guerrero, < 200 m ____ **D. salicifolia**
      4. Flowering female calyx tube 2.5–5.5 mm long (1.8–2 mm long in one Central American subsp.); lower lamina surface sparsely to densely hairy when mature, or if glabrate, then with swollen remnant hair bases conferring a papillose appearance; widespread in Mesoamerica.
         5. Lamina lanceolate or ovate, sometimes oblanceolate, obovate, or elliptic, abaxial vestiture consisting of hairs with swollen bases, conferring a distinct papillose appearance to the lamina, especially in glabrate leaves, the stomatal apparatus nearly always opaque and conspicuous; 2°–3° veins slightly impressed above with a raised vein-lamina seam; fruiting pedicels 2–16 mm long; fruiting calyx tube 2.5–5.5 mm long (tube : pedicel length = 0.2–1.2 : 1); plants often tall and slender; Yucatan Peninsula, Chiapas, Tabasco, SE Veracruz, Mexico, Belize, Guatemala, and NW Honduras, < 270(–1400) ____ **D. yucatanensis**
         5. Lamina oblanceolate to obovate, sometimes elliptic, abaxial surface without conspicuous papillae, or the papillae minute and diffuse (except in one rarely collected subsp. of *D. aequoris* from Honduras), the stomatal apparatus unobvious to opaque and conspicuous; 2°–3° veins usually flush to slightly raised above; fruiting pedicels usually < 6 mm long; fruiting calyx tube 4.5–10 mm long (tube : pedicel length = 1.1–18 : 1); plants not markedly tall and slender; Jalisco, Mexico to Panama, not known from the Yucatan Peninsula, < 1500 m ____ **D. acapulcensis**

1. Diospyros acapulcensis Kunth, Nov. Gen. Sp. 3:254. 1818. (**Fig. 2a–b**). *Macreightia acapulcensis* (Kunth) A. DC. Prodromus Systematis Naturalis Regni Vegetabilis 8:221. 1844. *Maba acapulcensis* (Kunth) Hiern, Trans. Cambridge Philos. Soc. 12:128. 1873. TYPE: MEXICO. GUERRERO: "Amérique Équatoriale" [as on label], "Crescit in litore occidentali Novae Hispaniae, prope Acapulco," "Fructificat Februario" [in protologue], *Humboldt & Bonpland s.n.* (LECTOTYPE, here designated: P-307187, digital image!).

Trees, arborescent shrubs or shrubs, (1–)2–12(–25) m tall, sometimes multi-stemmed clones, facultatively deciduous, mostly dioecious, rarely flowers of both sexes in the same inflorescence (the mating system in need of more study); **trunk** up to 40 cm dbh, bark ± smooth (not slick) to irregularly roughened, or patchy, often lichen encrusted (at least in W Mexico), often in part irregularly scaly, shallowly fissured or checked, especially at major branch forks, coloration uniform to patchy, usually grayish; **wood** yellowish to light brown when dry, reportedly very hard, slash nearly white to light yellow, rapidly turning yellowish, sap clear; **mature stems** terete to subterete, rarely angular, nearly smooth to roughened, fissured, half-netted, verrucose, or knotted, ± glabrous, the epidermis grayish, reddish, or brownish, lenticels often present, minute, circular, and bump-like to large and elliptic, sometimes fissure-like and forming a reticulum; **2nd year stems** terete to angular, smooth to half-netted, the bark sometimes sloughing, often longitudinally ridged, minutely fissured, bumpy, or verrucose, glabrous to sparsely hairy, rarely moderately to densely hairy, often with remnants of desiccated hairs, these sometimes coated with exudate, the epidermis viscid, often black gland dotted, occasionally mottled with reddish-brown or black, lenticels usually present; **1st year stems** quadrangular to subterete, smooth to verrucose, sometimes sulcate, sparsely to densely hairy, the hairs straight, wavy, curly, kinked, distally curved or hooked, 0.2–2 mm long, spreading to appressed, sometimes retrorse, hairs often reddish (the hairs throughout the plant are mostly simple glandular hairs, translucent in life, but variously colored in herbarium specimens due to darkening of a fluid in the lumen), clavate glandular hairs often present, deciduous, leaving the epidermis viscid, the epidermis green in life, grayish, reddish, or brownish in dry material, sometimes minutely lenticellate, *bud scales* ovate, concave, covered with appressed hairs. **Leaves** alternate, simple, entire; **petioles** (2–)4–7(–9) mm long, sometimes minutely winged, glabrous to densely hairy, clavate glandular hairs also sometimes present, these deciduous, leaving the epidermis viscid, sometimes without clavate glandular hairs and the epidermis dull, surface smooth to rugose, sometimes glaucous, pruinose or scintillant, lower surface convex, upper surface slightly concave or shallowly canaliculate to convex; **lamina** chartaceous to subcoriaceous, membranaceous when mature in one subspecies (shade and spring leaves often membranaceous), 45–125(–160) mm long, (15–)18–60(–65) mm wide, the length to width ratio (1.7–)2–3.6(–4.4) : 1, mostly oblanceolate to obovate, sometimes elliptic, oblong or oval, usually slightly wider in the distal half, sometimes obtrullate, rarely lanceolate or ovate, clavate glandular hairs often present, deciduous, leaving the epidermis viscid, the epidermis color variable, but darker above, *base* cuneate to long or short attenuate, decurrent on the petiole, *margin* flat to revolute, sometimes ciliate, *apex* acute to obtuse, acuminate or tapered to a blunt point, rounded, or mucronulate; **lower lamina surface** sparsely to densely hairy, rarely glabrate, the hairs variable, often deciduous, the epidermis often viscid, coloration sometimes mottled, the stomatal apparatus clear or off-white, opaque, and conspicuous, and then may be mistaken for scales; **upper lamina surface** glabrous to moderately hairy, the hairs often wavy and upright to ascending, usually deciduous, their bases sometimes thickened, annular seeping glands sometimes appearing where hairs have fallen, stellate hairs occasionally present, often crystal-papillose (with aggregates of opaque off-white excrescences), more obviously so in thinner leaves (rarely on the abaxial lamina surface), sometimes tented (with minute well spread-out waves or peaks along veins of the lamina surface caused by differential drying in herbarium specimens). **Venation** arcolanguid (Provance & Sanders 2005) to brochidodromous, sometimes eucamptodromous, 3(–5)-ribbed, often darkened on the lower surface of young leaves; **midrib** usually prominent below, glabrate to densely hairy, smooth to rugose, sometimes glaucous, pruinose or scintillant, slightly impressed to convexly-raised above near the base, flush to slightly raised distally, usually impressed along the lamina-midrib seam, hairs tending to be upright, clavate glandular hairs often present, deciduous, leaving the epidermis viscid; **lateral veins** 5–12 on each side of the midrib, often the basal pair and/or the second from the base, diverging from the midrib at a more acute angle and with a straighter course than the others, raised below, flush to slightly raised above; **3° veins** obscure to conspicuously raised below, usually flush or inconspicuously raised above; **4°–5° veins** obscure to barely raised. **Laminar extrafloral nectaries** nearly always present on the lower lamina surface (very rarely on the upper surface), tending to be near the midrib in the proximal

half of the lamina, minutely rimmed, flat to concave, slightly raised to sunken in the lamina, elliptic, round or amorphic, mostly 0.3–1.5 mm in longest dimension, green in life, drying greenish, reddish, brownish or black. **Male inflorescences** solitary (2–)3–5(–7)-flowered cymes in leaf axils of young (usually 1st year) stems, cymes of male flowers rarely terminated by a female flower, moderately to densely hairy, the hairs minute, nearly straight to wavy or kinked, upright to ascending, tawny or dull orange to reddish or dark brown, epidermis sometimes viscid, straw, yellowish, dull orange, light brown, golden brown, reddish-brown, or dark brown; **peduncles** 1–6 mm long, often angular; **pedicels** 0.5–3 mm long, broadening distally, bracts linear-elliptic to ovate, 1–2.5 mm long, often navicular. **Male flowers** 3–4-merous; **male flowering calyx** narrowly campanulate to campanulate or infundibuliform, exterior hairs moderate to dense, sometimes glabrous near the sinuses, the hairs minute, otherwise as variable as those of the stems (but not retrorse), clavate glandular hair sometimes present, epidermis often viscid, *tube* (1.5–)2–4 mm long, 3(–4) mm wide, sometimes keeled from sinus to the base, *lobes* valvate-reduplicate in the bud, lanceolate to ovate, 1.5–6 mm long, 1.5–4 mm wide, apex acute, sometimes acuminate; **male corolla** in life white, cream, yellow, or red (reportedly, perhaps in error) in life, the exterior hairs in dry material off-white, pinkish, tawny, yellowish, orangish, reddish or brownish, interior glabrous; **male corolla tube** urceolate to narrowly urceolate, narrowing distally, (2.8–)3–7 mm long, 2–4 mm wide, with three shield-shaped, 1–2.5 mm long, glabrous zones at the base (shielded), or sometimes the basal 1/4–1/2 of the tube completely glabrous, otherwise sericeous with an undercoat of minute curly to straight hairs, minute hairs (including occasional retrorse hairs) sometimes present between the sericeous and glabrous zones; **male corolla lobes** spreading in life, lanceolate, ovate, rhombic or elliptic, 2–3.5 mm long, 1–2.8 mm wide, hairs dense, minute, curly to wavy, with some straight intramarginal hairs, these sometimes retrorse, median sericeous, at least basally. **Stamens** 12(–14); **filaments** adnate to the corolla at or near the base, or inserted on the receptacle, or both, usually in tiers or groups of six stamens, sometimes geminate, 0.8–2 mm long; **anthers** lanceolate, ovate or oblong, 1.2–3 mm long, apex acuminate, rostrate, aristate, or bluntly pointed, opening by longitudinal slits. **Pistillode** minute, densely hairy, the hairs wavy to straight. **Female inflorescences** solitary flowers in leaf axils of young (often 1st year) stems, rarely 3-flowered cymes; **female flowering pedicels** with hairs and epidermis similar to male inflorescences. **Female flowers** 3–4(–5)-merous; **female flowering calyx** mitriform, exterior moderately to densely hairy, the vestiture and epidermis the same as in male flowering calyces, interior vestiture similar to interior fruiting calyx, *tube* cupulate to cylindrical, 1.8–5.5 mm long, 3.5–5 mm wide, sometimes very thick, especially basally, *lobes* valvate-reduplicate in the bud, winged, broadly rounded to ovate, (2–)3–8.5 mm long, 4–10 mm wide, apex vaguely acuminate or bluntly acute, nerves sometimes conspicuous; **female corolla** range of coloration similar to that of male corollas; **female corolla tube** narrowly to short urceolate or subcylindrical, narrowing distally, 2.7–7 mm long, 2.3–3.5 mm wide, exterior vestiture similar to male corolla tubes, interior glabrous; **female corolla lobes** spreading in life, lanceolate to ovate or rhombic, 2–4 mm long, 1–2 mm wide, margins often glabrous and partly involute, exterior vestiture the same as for male flowers, interior glabrous; **ovary** depressed- globose to subglobose, turbinate, or obturbinate, 2–3 mm long, 1.5–4.5 mm wide, sometimes vaguely 3-lobed, sparsely hairy to sericeous, hairs variously colored, longer hairs sometimes present at the base, rarely with shield-shaped glabrous zones similar to those of the corolla tube; **styles** 3(–4), usually fused into a column part of the way and spreading distally, 1–3 mm long, usually densely hairy; **stigmas** bifid, about 0.8 mm long, exterior sometimes hairy. **Fruiting pedicels** terete to angular, often broader distally, 0.5–9 mm long, sometimes fissured or half-netted, sometimes lenticellate, vestiture persisting or becoming glabrous, epidermis often viscid, bracts (0–)1–2, alternate or opposite, lanceolate to broadly ovate or deltate, 1.2–2.5 mm long, 0.9–2.5 mm wide, flat, concave or navicular. **Fruiting calyx** slightly accrescent, campanulate or infundibuliform to explanate, the sinus sometimes tearing, exterior vestiture as described for flowering calyces or glabrate, often with pale desiccated remnants of original vestiture, epidermis often conspicuously viscid and darkened, *tube* (3–)4–10 mm long, sometimes bulbous at the base, interior sparsely to densely hairs, the hairs usually appressed to subappressed and distally directed, variously colored, hairy to the base

or glabrous in the lower 1/10–1/2, epidermis sometimes with dark blotches, *lobes* obtuse to rounded, rarely acute, reflexed (basally, near the apex, or along the margins) to ascending, (2–)3–7.5(–9) mm long, 7–15(–16) mm wide, apex usually abruptly acuminate to a blunt point, interior intramarginal band of hairs variable in width, the hairs usually dense, minute, wavy, curly or kinked, upright, epidermis usually viscid, hairs of the median usually dense, straight, appressed, and similar in color to those of the intramargin. **Fruit** a subglobose to depressed-globose berry, 1.5–3.5 cm in diameter, consistently with three pairs of locules; **flesh** gelatinous, sweet when ripe, with variable amounts of remnant astringency, becoming vitreous, red and translucent upon drying; **epidermis** smooth to orange-peel textured, glabrous to sparsely and weakly hairy when mature, a basal ring of subappressed, fine, straight hairs sometimes present (the ring sometimes adhering to the base of the calyx tube), the apex sometimes umbilicate, usually densely and minutely hairy, in life green when unripe and yellow, orange, or light brown when ripe, rarely red, in herbarium material yellow, dark yellow, orange, golden brown, or brown. **Seeds** 6, wedge-shaped (resembling an orange segment with rounded edges), 11–16 mm long, 5.5–8 mm radial depth, 3.5–6 mm wide, brick red to dark brown, texture rugulose-foveolate.

KEY TO THE SUBSPECIES OF *DIOSPYROS ACAPULCENSIS* IN MESOAMERICA

1. Fruiting pedicels 0.3–1 mm long; lamina obtrullate, 40–50 mm wide at 3/4 length, reddish-brown, densely hairy below when young, glabrate when mature, the curly to slightly wavy hairs with swollen bases, leaving annular glandular papillae after the hairs fall; fruiting calyx nearly black, glabrescent to sparsely hairy, lobes 12–13 mm wide, apices reflexed; pine forests of SW Honduras, 750–1120 m _____ subsp. **mejocotensis**
1. Fruiting pedicels > 2 mm long; lamina rarely obtrullate, rarely over 45 mm wide at 3/4 length; color and vestiture of lamina and fruiting calyx variable; fruiting calyx lobes 7–16 mm wide, apices reflexed or not; Jalisco, Mexico to Panama, including Honduras.
   2. Fruiting calyx lobes 7–7.5 mm long, base of calyx tube swollen; mature lamina (e.g. in fruiting specimens) membranaceous to subchartaceous, apex narrowly acute to narrowly acuminate, base narrow (length **:** width at 0.25 c. 5 **:** 1), abaxial hairs straight, appressed, distally directed; male cymes terminated by female flowers; anthers yellow with red dots; Chiquimula vicinity, SE Guatemala, 400–1000 m _____ subsp. **chiquimulensis**
   2. Fruiting calyx lobes usually 3–6 mm long, base of calyx tube swollen or not; mature lamina chartaceous (rarely membranaceous or subcoriaceous), apex rounded to acute, sometimes acuminate, but not narrowly acuminate (except in subsp. *dwyeri*, and sometimes in subsp. *veraecrucis*), less narrowed basally (except in subsp. *dwyeri*) (length **:** width at 0.25 usually < 5 **:** 1), abaxial hairs variable; inflorescences not as described above; anthers not red dotted; Jalisco, Mexico to Panama, including Guatemala.
      3. Hairs of lower lamina surface straight, appressed, distally directed.
         4. Fruiting pedicels > 6 mm long; fruiting calyx lobes < 9.5 mm wide; leaves narrow, especially basally (length **:** width at 0.25 > 5.5 **:** 1); known only from Panama_____subsp. **dwyeri**
         4. Fruiting pedicels < 6 mm long; fruiting calyx lobes mostly > 10 mm wide; lamina sometimes narrow, but less narrow basally (length **:** width at 0.25 usually < 5 **:** 1), Mexico to Costa Rica.
            5. Lower lamina 3° venation not raised, sometimes apparent due to darkened coloration, the span of the four centermost lateral veins usually < 40 mm; petioles 2–6 mm long; lamina 45–105(–120) mm long, width at 0.75 length 15–29 mm; fruiting calyx tube mostly 5.5–9 mm long, the lobes 9–15.5 mm wide; S Mexico (except the Yucatan Peninsula), W Guatemala and El Salvador, < 1240 m _____ subsp. **veraecrucis**
            5. Lower lamina 3° venation prominently raised, the span of the 4 centermost lateral veins usually > 40 mm; petioles 4–8 mm long; lamina 78–130(–150) mm long, width at 0.75 length (21–)24–40 mm; fruiting calyx tube 3.5–7 mm long, the lobes 6.5–13 mm wide; often near the Pacific Coast of Nicaragua and NW Costa Rica, < 150 m (rarely to 600 m) _____ subsp. **rivensis**
      3. Hairs of lower lamina surface curly to straight, not appressed, not strictly distally directed.
         6. Lower lamina reddish-brown, the vestiture (including the midrib) dense, the hairs curly or kinked, golden-brown to reddish-brown; petioles rugose, glaucous-pruinose and mauve to dark purple; fruits up to 35 mm in diameter; gallery forests, mostly WC Nicaragua_____ subsp. **pedromorenoi**
         6. Lower lamina (including the midrib) epidermis and vestiture color various, glabrate to densely hairy, the hairs straight to wavy; petioles not as above; fruits < 30 mm in diameter; W Mexico, Guatemala, Honduras, Nicaragua, and Costa Rica (one subsp. rare in El Salvador).
            7. Lamina often elliptic, length **:** width 2.1–3.8 **:** 1; adaxial lamina surface often laden with clusters of opaque white crystals (crystal-papillose), and often with minute peaks and waves along veins

caused by differential drying (tented); hairs on the abaxial midrib surface appressed to subappressed; coastal Nicaragua and Costa Rica, < 150(–600) m _____ subsp. **rivensis**

7. Lamina oblanceolate to obovate, rarely elliptic, length : width 1.7–2.7(–3.3) : 1; adaxial lamina surface crystal-papillose or not, sometimes tented; hairs on the abaxial midrib surface ascending, spreading or retrorse; W Mexico, Guatemala, Honduras, Nicaragua, and Costa Rica (one subsp. rare in El Salvador).
   8. Hairs of inflorescence dense, gold to reddish-gold; hairs of the upper lamina similar, but with swollen bases, deciduous, leaving seeping annular papillae; fruits often dark brown; endemic to Costa Rica _____ subsp. **guanacastensis**
   8. Hairs of inflorescence and leaves not as above; fruits not drying dark brown; plants of W Mexico, Guatemala, Honduras, Nicaragua, and rarely El Salvador (subsp. *nicaraguensis*).
      9. Fruiting calyx glabrous inside near the base, lobes usually ≤ 10.5 mm wide; lamina (63–)82–140 mm long, mostly (20–)29–50(–63) mm wide, 24–43(–47) mm wide at 0.75 length; SE Guatemala, Honduras, Nicaragua, rarely collected in El Salvador _____ subsp. **nicaraguensis**
      9. Fruiting calyx hairy inside to the base, lobes rarely < 11 mm wide; lamina 50–82(–127) mm long, usually (18–)23–39(–44) mm wide, < 29 mm wide at 0.75 length; W Mexico and W Guatemala _____ subsp. **acapulcensis**

1a. Diospyros acapulcensis Kunth subsp. **acapulcensis**. (**Figs. 2a–b, 3, 4, 5, 19c**).

Trees to shrubs, 2–14 m tall; **trunk** to 30 cm dbh., bark light grayish-brown; **stems** glabrous to sparingly hirsutulous, young stems puberulent and wavy-hairy. **Petioles** (2.5–)3.5–6(–7) mm long, glabrous to densely hairy, the hairs wavy to straight, ascending to retrorse, sometimes glandular above. **Lamina** chartaceous, 50–105(–128) mm long, (18–)23–39(–44) mm wide, length to width ratio (1.8–)2–2.8(–3.3) : 1, oblanceolate to obovate, sometimes nearly elliptic, *base* cuneate to acutely rounded, sometimes attenuate, decurrent on the petiole, *margin* flat to minutely revolute, *apex* acute to broadly acuminate, occasionally rounded; **lower lamina surface** sparsely to densely hairy, the hairs straight to wavy, ascending to upright, not strictly apically directed, clavate glandular hairs present, but deciduous; epidermis dull light brownish- green, the stomatal apparatus translucent, sometimes opaque and conspicuous; **upper lamina surface** sparsely to densely erect-villous, epidermis sometimes crystal-papillose. **Venation** brochidodromous to arcolanguid; **midrib** pubescent or hirsute to wavy-hairy below, especially along the sides, the hairs sometimes ascending, tawny or orangish, finer above, sometimes retrorse basally; **lateral veins** 5–8 per side, prominent below, flush to raised and apparent above; **3° veins** barely raised below, flush or slightly raised above. **Male inflorescences** 1–3(–5)-flowered cymes; **peduncles** 1–2 mm long; **pedicels** 1.5–2 mm long, bracts oblong-lanceolate, 1–2 mm long, navicular. **Male flowering calyx** sericeous inside to the base to glabrous, ascending wavy-tomentulose outside, epidermis viscid and dark, *tube* 2–4 mm long, 3–3.5 mm wide, *lobes* acute, 2–4 mm long, 2–3 mm wide; **male corolla tube** 3.5–6.5 mm long, 2–3 mm wide, exterior basal 1/3 glabrous, otherwise tawny sericeous, bordering region scantily retrorse-puberulent; **male corolla lobes** lanceolate to oblong-ovate, 2 mm long. **Stamens** 12; **filaments** adnate in two tiers to the corolla, the inner basal, the outer tier just above, 1–1.8 mm long; **anthers** oblong-ovate, 2 mm long, rostrate. **Female inflorescences** densely hairy, bracts opposite, 1.5–2 mm long, similar to male bracts. **Female flowering calyx** short-mitriform, interior cream to tawny sericeous to the base, the intramarginal band wide, exterior tomentulose, with scant slightly longer, wavy, ascending hairs, *tube* cupulate, thickened near the base, 4–5.5 mm long, 4.5–5 mm wide, *lobes* broadly rounded, (2–)4–8 mm long, 8–10 mm wide; **female corolla tube** 5.5–6 mm long, 3 mm wide, exterior lower 1/2 glabrous, upper 1/2 sericeous, the bordering region scantily retrorse-puberulent; **female corolla lobes** lanceolate to ovate, 2.5 mm long, 1.3 mm wide; **ovary** depressed-globose, 2.5 mm long, 4.5 mm wide, minutely cream sericeous; **styles** 3, ± 1.8 mm long, partly fused, densely hairy; **stigmas** vaguely bifid, 0.8 mm long, minutely appressed hairy; **staminodes** (3–)6(–9), adnate to the corolla from the base to mid-tube, the free portion 1.2–1.4 mm long, sometimes inserted on the receptacle, the sterile anthers knife-shaped, 1 mm long, basally asymmetric, the filament flattish. **Fruiting pedicels** stout, 1–4.5(–6) mm long. **Fruiting calyx** rotate to campanulate, often splitting at the sinuses, exterior glabrate or with persisting desiccated hairs, epidermis viscid, dark brown, *tube* (5–)6–10

Fig. 4. Trunk of *D. acapulcensis* subsp. *acapulcensis*. Chorros del Varal, Jalisco/Michoacan, with ± smooth bark except in the branch fork where shallowly checked.

mm long, often bulbous near the pedicel, *lobes* obtuse, (2–)4–7(–9) mm long, (9.5–)11–15(–16) mm wide, reflexed, margins sometimes reflexed. **Fruit** subglobose to depressed-globose, 1.5–2 cm long, 1.5–2.5 cm in diameter, with slightly wavy to straight golden subappressed hairs at the base, these dense at the apex, epidermis often glaucous-pruinose and/or scintillant, yellowish to golden brown. **Seeds** 11–14 mm long, 6–8 mm radial depth, 4–5 mm wide.

Diospyros acapulcensis subsp. *acapulcensis* is nearly endemic to western and southwestern Mexico, but is unknown from Oaxaca (Fig. 23), and is known elsewhere only from a single collection from Guatemala. It is an infrequent to occasional component of matorral, tropical deciduous forest, seasonal evergreen forest, and oak forest, in canyons and on slopes and mesas below 1350 m. Like many taxa in the complex, it may persist or be spared along roadsides and at the edges of cultivated land. It resembles *D. a.* subsp. *veraecrucis*, but is differentiated by the abaxial lamina pubescence (see subsp. *veraecrucis*) and the shape of the lamina. It also closely resembles *D. a.* subsp. *nicaraguensis*, but that differs in having a lamina that tends to be longer and wider, narrower fruiting calyx lobes, and a calyx tube that is usually not sericeous inside to the base.

Representative specimens. **GUATEMALA. Huehuetenango:** Sierra de los Cuchumatanes, 800–1200 m, 30 Aug 1942, *J.A. Steyermark 51584* (F). **MEXICO. Chiapas. Mpio. Chiapa de Corzo:** above El Chorreadero, 800 m, 11 Aug 1972, *D.E. Breedlove 26874* (MO, CHAPA).

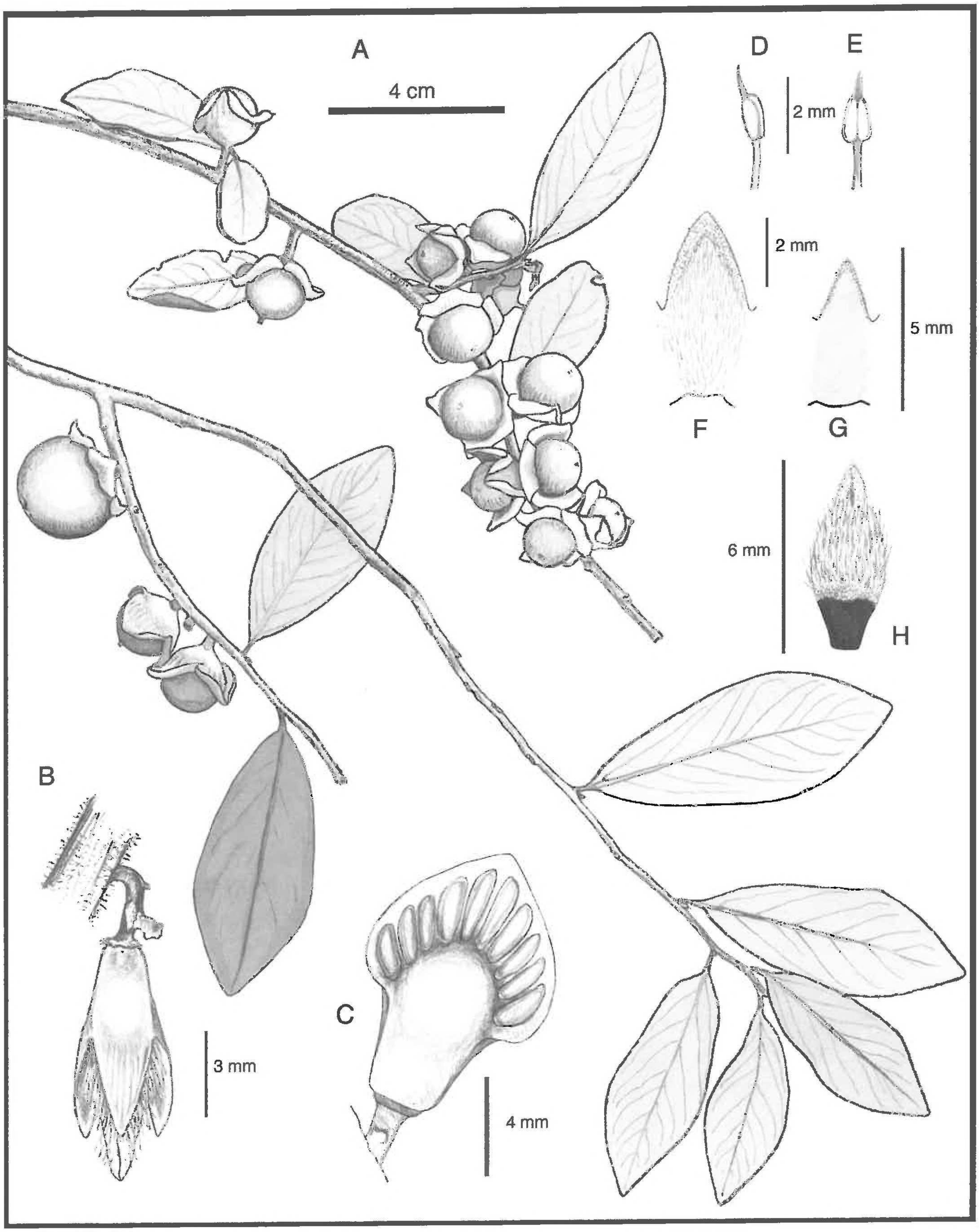

Fig. 5. Diospyros acapulcensis subsp. acapulcensis. A. Fruiting branchlets (M.C. Provance et al. 9398, UCR). B. Male flower (G.B. Hinton et al. 6044, MO). C. Female immature flower (J. Steyermark, F). D–E. Based on E. Carranza & E. Perez C. 4743 (IEB). D. Stamen (lateral view). E. Stamen (adaxial view). F. Adaxial surface of male calyx (Kruse 1636, MO). G–H. Based on J. Rzedowski 22806 (MSC). G. Adaxial surface of male calyx. H. Immature male corolla.

Mpio. Terán: 6.5 km W of Tuxtla Gutiérrez, 600 m, 8 Oct 1971, *D.E. Breedlove 20121* (MO). **Mpio. Tonalá:** Tonalá, 100 m, 6 May 1988, *J.I. Calzada 13814* (XAL). **Mpio. Tuxtla Gutiérrez:** Tuxla Gutiérrez–El Sumidero, km 16, 990 m, 19 May 1982, *J.I. Calzada 9223* (IEB, XAL). **Mpio. Tzimol:** 15 km S of Comitan, 1200 m, 19 Nov 1980, *D.E. Breedlove & F. Almeda 47619* (MO). **Mpio. Venustiano Carranza:** above Soyatitán, 3400 ft, 25 Oct 1967, *A. Shilom Ton 3105* (CAS). **Mpio. Villa Corzo:** near El Brillante, 650 m, 9 Oct 1974, *D.E. Breedlove 38411* (MO). **Colima. Mpio. Comala:** cerca de Campo Cuatro, 1200–1300 m, 5 May 1998, *R. Cuevas 5858* (ZEA). **Mpio. Tecoman:** 1.5–2.5 km de la empresa "Apasco," 400–560 m, 6 Apr 1996, *R. Cuevas & L. Guzmán 5133* (ZEA). **México. Mpio. Temascaltepec:** Palmar, 13 May 1934, *G.B. Hinton et al. 6044* (MO). **Guerrero. Mpio. Acapulco de Juarez:** Río Papagayo, 3 km NW de Xalapa, 200 m, 17 Jan 1994, *R. Fernandez N. 4929* (IEB). **Mpio. Chilpancingo:** Salto Valadéz, 1350 m, 25 Jan 1970, *H. Kruse 2692* (MO); al N de Acahuizotla, camino a Palo Blanco, [17°23'N, 99°27'W], 930–1050 m, 19 Jan 1994, *E. Carranza & E. Perez C. 4743* (IEB). **Mpio. Iguala:** E de Tierra Colorada, 300 m, 8 Jul 1966, *J. Rzedowski 22806* (MSC). **Mpio. Mochitlán:** Agua de Obispo, barranca del Cuarenta, 945 m, 15 Jul 1967, *H. Kruse 1636* (MO). **Mpio. San Marcos:** Piedra Grande, 310 m, 31 Jan 1983, *J.S. Miller & P. Tenorio L. 553* (MO). **Mpio. Taxco:** 7 mi N of "Centro" sign at Iguala, 25 Jan 1971, *J. Freeland & L. Spetzman 50* (ARIZ, NA). **Jalisco. Mpio. Autlan de Navarro:** Arroyo El Coajinque, 1000 m, 3 Oct 1998, *R. Cuevas 5872* (ZEA). **Mpio. Casimiro Castillo:** camino Piedra Pesada–Rancho Los Patos, 395 m, 18 Nov 2000, *R. Cuevas 6910* (ZEA). **Mpio. El Grullo:** Arroyo El Colomo, 1000 m, 7 Nov 1988, *F. Santana M. & W. Anderson 4068* (ZEA). **Mpio. Puerto Vallarta:** cerca Fracc. Colinas Campestres, 150 m, 26 Aug 1990, *M, Cházaro B. & O. Montes 6405* (IEB, UCR). **Mpio. San Sebastián del Oeste:** 18 km WNW of San Sebastian, 410 m, 7 Jan 1990, *T.S. Cochrane et al. 12026* (IEB). **Mpio. Santa Maria del Oro:** Santa Maria del Oro, 900 m, 19 Dec 2005, *I. Garcia R. & M.C. Provance 7359* (CIMI, UCR). **Mpio. Tolimán:** 8–9 km adelante de Campo Cuatro, 1400 m, *R. Cuevas 4039* (ZEA). **Michoacan. Mpio. Aquila:** 3 km E de Aquila, 250 m, 29 Feb 1980, *B. Guerrero C. 742* (XAL). **Mpio. La Huacana:** Limón del Jorullo, 690 m, 15 Jun 2002, *X. Madrigal S. & S. Ontivaros A. 4803* (EBUM). **Mpio. Los Reyes/Periban (Jalisco):** Chorros del Varal, 950–1000 m, 30 Jun 2005, *I. García et al. 7122* (CIMI, UCR); Puente de Iturria, 28 Jun 2004, *M.C. Provance et al. 9398* (UCR). **Morelos. Mpio. Tepalcingo de Hidalgo:** 1 km SE de El Limón, 1310 m, 25 Feb 1991, *J. Bonilla 1434* (IEB, UCR).

1b. **Diospyros acapulcensis** Kunth subsp. **chiquimulensis** M.C. Provance, I. García & A.C. Sanders, subsp. nov. (**Figs. 6, 19a–b**).

Type: GUATEMALA. Chiquimula: "Frecuente a la entrada de Chiquimula," [ca. 14°48'N, 89°33'W], "100 m" [probably 400–1000 m], 20 May 1963, *A. Molina R. & A.R. Molina 12473* (holotype: F-1622586!).

Arbores a *Diospyros acapulcensi* ssp. *acapulcensi* similis sed differt laminis foliorum majoribus tenuioribus, infra strigosis trichomatibus rectis adpressis apicem versus, inflorescentiis floribus staminatis et pistillatis, calycis pistillatis intus ac tubis corollarum pistillatarum extus dense strigosis trichomatibus rectis horizontalibus, et antheris flavis erythrostictis differt.

Trees 4–5 m tall; **trunk** unknown; **stems** glabrous to sparsely hairy, the young stems sparsely hairy, the hairs apically curved to slightly wavy and subappressed, clavate glandular hairs present. **Petioles** minutely winged, 4 mm long, glandular-viscid, appressed to subappressed-puberulent below, sparsely ascending-puberulent above. **Lamina** membranaceous to subchartaceous, 80–103 mm long, 25–35 mm wide, length to width ratio 3–4 **:** 1, oblanceolate, *base* acute to narrowly cuneate, decurrent on the petiole, *margin* ± flat, ciliate, *apex* narrowly acute to narrowly acuminate; **lower lamina surface** sparsely to moderately appressed-pubescent, clavate glandular hairs also present, especially basally, the epidermis light brown, the stomatal apparatus translucent and inconspicuous; **upper lamina surface** glabrate, clavate glandular hairs sometimes present, the epidermis dark brown, densely papillate, somewhat tented. **Venation** brochidodromous; **midrib** subprominent below, with scant minute, appressed hairs, sparsely and minutely hairy above, sometimes with deltoid scales, glandular-viscid; **lateral veins** 9–12 per side, fine below, slightly raised above; **3°–4° veins** darkened below, inconspicuous above. **Male inflorescences** 3–4(–7)-flowered cymes (terminated by a female flower), densely minutely hairy; **peduncles** 2.5–3.5 mm long; **pedicels** 1–2 mm long, bracts lance-ovate, 2–2.5 mm long, navicular. **Male flowering calyx** finely subappressed wavy-hairy outside, epidermis dark brown, viscidulous, *tube* 3 mm long, 3 mm wide, often keeled from sinus to base, mostly glabrous inside, *lobes* ovate, 3.5–4 mm long, 4 mm wide, slightly winged, acuminate to a point, glandular, mostly sericeous inside; **male corolla tube** 2.8 mm long, 2 mm wide, thick-walled, exterior base with three glabrous shield-shaped zones, upper 1/2 densely buff sericeous; **male corolla lobes** (immature) thick, lanceolate, 1.5 mm long, 1 mm wide. **Stamens** 12; **filaments** adnate to the corolla towards the base, but at unequal levels, 1 mm long, sometimes geminate, *connective* red; **anthers** lanceolate to lance-acuminate, 1.5–2 mm long, yellow with minute red dots. **Female inflorescences** solitary flowers (those seen somewhat immature), or terminal flowers in otherwise male inflorescences, bracts lanceolate, up to 2.5 mm long, ± keeled. **Female flowering calyx** densely hairy outside, the hairs minute, slightly wavy, golden, *tube* 4 mm long, 3.5 mm wide, very thick, especially near the base, glabrous inside near the base, otherwise densely straight-hairy,

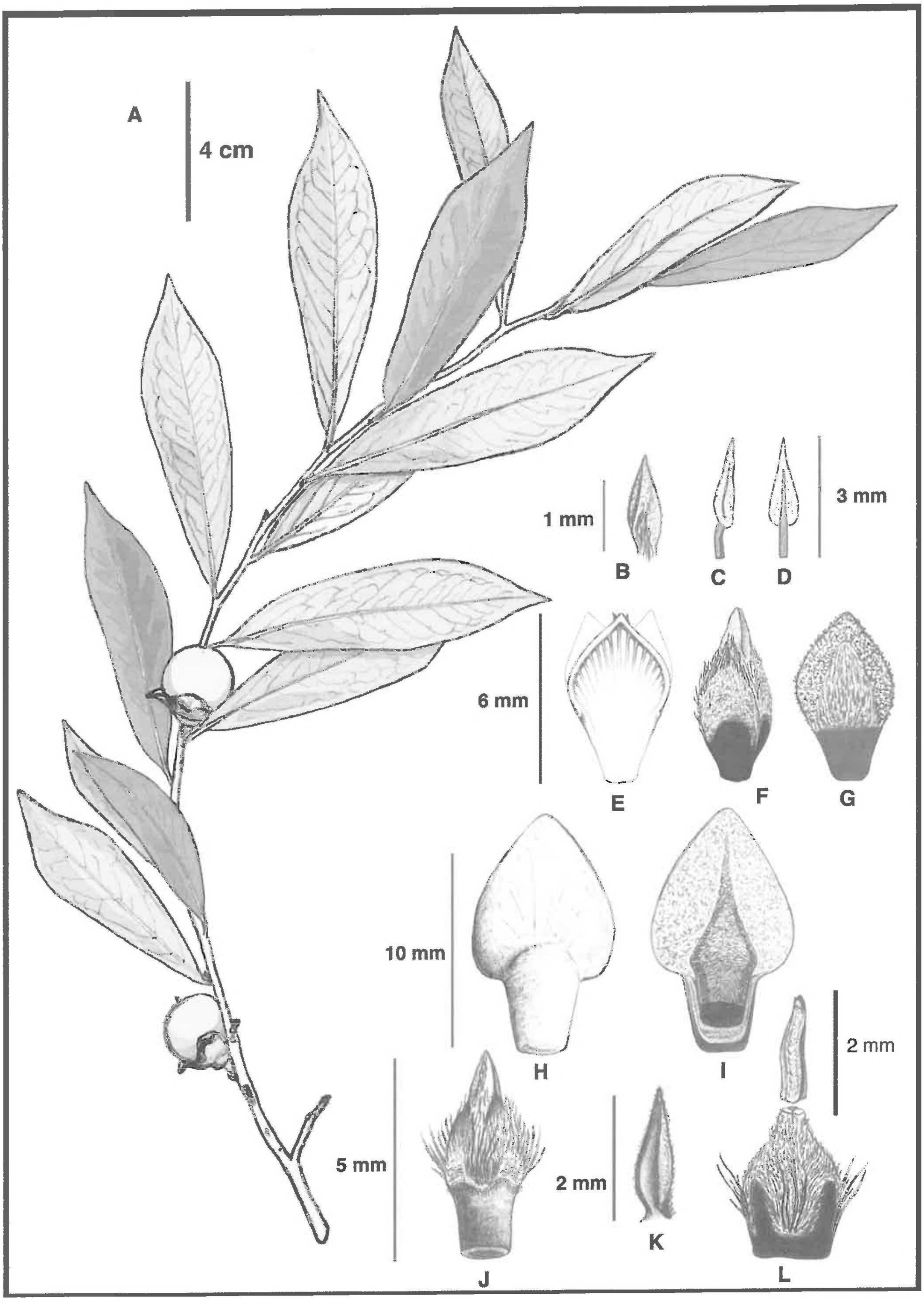

Fig. 6. *Diospyros acapulcensis* Kunth subsp. *chiquimulensis* M.C. Provance, I. García & A.C. Sanders, subsp. nov. Based on the holotype (*A. Molina R. & A.R. Molina 12473,* F-1622586). **A.** Fruiting branchlet. **B.** Male corolla lobe (abaxial side). **C.** Stamen (lateral view). **D.** Stamen (adaxial view). **E.** Immature male flower. **F.** Immature male corolla. **G.** Adaxial surface of immature male flowering calyx. **H.** Abaxial surface of immature female flowering calyx. **I.** Adaxial surface of immature female flowering calyx. **J.** Immature female corolla. **K.** Female corolla lobe (adaxial side). **L.** Pistil.

these horizontally oriented, reddish-gold, *lobes* 8.5 mm long, 7.5 mm wide, intramarginal band relatively wide, hairs golden, median hairs horizontally and distally oriented, the epidermis dark; **female corolla tube** 6–7 mm long, exterior lower 1/2 glabrous, upper 1/2 with three evenly spaced sericeous areas, the hairs of the intervening regions minute, horizontally oriented, upper and lower-halves separated by an undulate ring of minute retrorse hairs, epidermis dark reddish-brown; **female corolla lobes** lanceolate, 2–2.3 mm long, 1 mm wide; **ovary** subglobose, 2 mm long, 1.5 mm wide, minutely cream sericeous, with clusters of longer hairs from the base, three shield-shaped glabrous zones also present around the base; **styles** 3, fused into a 1.5 mm long column, minutely hairy; **stigmas** unknown (damaged); **staminodes** 3, lanceolate, adnate to the corolla. **Fruiting pedicels** stout, ± 3 mm long, densely hairy. **Fruiting calyx** campanulate to infundibuliform, similar outside to the flowering calyx, *tube* 5–6 mm long, bulbous at the base, *lobes* obtuse, 7–7.5 mm long, 11 mm wide, reflexed near the apex. **Fruit** (probably immature) ± 1.5 cm diameter, moderately hairy, the hairs minute, subappressed, nearly straight, gold, epidermis glaucous-pruinose, light golden brown. **Seeds** unknown.

This taxon is notable for male flowering cymes terminated by female flowers; its large, thin, leaves with acuminate apices coming to distinct points; horizontal hairs on the inside of the female calyx and the outside of the female corolla tube; and yellow anthers with red dots. Further study may reveal that this taxon warrants species rank, but we are following a conservative course in placing it at the subspecific level, because we've only seen a single specimen. Of related taxa, it is most similar to *D. a.* subsp. *veraecrucis*. The single collection was made near Chiquimula, Guatemala, at an elevation of "100 m" (Figs. 23, 24). The reported elevation is likely a typographical error for 1000 m, as the lowest elevation in the area is 400 m. This species is named for the Department of Chiquimula, Guatemala, where the type specimen was collected.

1c. Diospyros acapulcensis Kunth subsp. **dwyeri** M.C. Provance, I. García & A.C. Sanders, subsp. nov. (**Figs. 7, 21c**). TYPE: PANAMA. PANAMA: Canal Zone, Farfan Beach, road along beach, [8°56'N, 79°35'W, 1–5m], 3 Aug 1967, *J.D. Dwyer & S.M.V. Hayden 7525* (HOLOTYPE: MO-2067635!; ISOTYPES: MO-2129488!, F! online image, UC, COL, "Moldenke" [probably at LL]).

Frutices a *Diospyros acapulcensi* ssp. *acapulcensi* similis sed differt petiolis fructiferis longioribus, lobis calycibus angustioribus, et laminis foliorum amplioribus quoad rationi longitudo-latitudo infra strigosis trichomatibus rectis adpressis apicem versus.

Shrubs to 4.5 m tall; **trunk** unknown; **stems** glabrous when mature, young stems sparsely upright to subappressed-villous and densely covered in shorter upright to ascending, curved to kinked, yellowish to golden-brown hairs, the epidermis glistening, brownish mottled. **Petioles** minutely winged, 4–5 mm long, yellowish, hairy below, densely and conspicuously yellowish hirsutulous to pubescent above. **Lamina** subchartaceous to chartaceous, 60–70(–80) mm long, 15–20 mm wide, length to width ratio 3.2–4 : 1, oblanceolate, *base* cuneate to narrowly acute, decurrent on the petiole, *margin* flat to minutely revolute, *apex* narrowly acuminate with a blunt point; **lower lamina surface** sparsely ± appressed-pubescent, the hairs 0.5–1.5 mm long, densest near the margin, clavate glandular hairs present, the epidermis tan to light greenish-brown, the stomatal apparatus translucent and inconspicuous; **upper lamina surface** sparsely puberulent, the epidermis brownish-green, even to vaguely tented, densely crystal-papillose. **Venation** arcolanguid; **midrib** prominent below, subappressed to appressed puberulent, the hairs mostly > 1 mm, yellowish, clavate glandular hairs present, on the upper surface flush to slightly raised, puberulent to short wavy-hairy, the epidermis yellowish; **lateral veins** 6–8 per side, yellowish, prominent below, apparent above; **3°–4° veins** fine and barely raised below, sometimes darkened, inconspicuous above. **Male inflorescences and flowers** unknown. **Female inflorescences and flowers** unknown, except **style remnants** on immature fruit columnar, ± 3 mm long, minutely hairy. **Fruiting pedicels** slender, 6–8 mm long, bracts narrowly oblong, minute, concave to navicular. **Fruiting calyx** densely hairy outside, the hairs minute, wavy, subappressed to ascending, reddish-gold, epidermis dark, *tube* half-globose, 4–6 mm long, sparsely golden sericeous inside, *lobes* spreading, rounded, 4–5 mm long, 7–9 mm wide, acuminate to an obscure point, interior mostly reddish-gold sericeous, golden tomentulose at the intramargin. **Fruit** (immature) globose, the hairs straight to curved, 0.1–0.5 mm long, appressed to subappressed except basally where straight, fine, ± 1 mm long, epidermis dark reddish-brown. **Seeds** unknown.

Fig. 7. Holotype of *D. acapulcensis* Kunth subsp. *dwyeri* M.C. Provance, I. García & A.C. Sanders, subsp. nov. (*J.D. Dwyer & S.M.V. Hayden 7525*, MO-2067635).

This subspecies seems endemic to Panama, the only collection seen being from Farfan Beach, near the Pacific entrance to the Panama Canal (Fig. 24). Vegetation mapped in this area includes semideciduous forest and periodically inundated tree savanna with a grassy herb layer (ANAM and CBMAP 2000). There may also be patches of swamp forests in the vicinity. Unseen collections of '*Diospyros salicifolia*' cited for Panama (White 1978, D'Arcy 1987) may represent this subspecies, and include a collection from Cativo Swamp, Darien Province (*Duke 11739a*). This taxon is easily separated from *D. a.* subsp. *veraecrucis* by its much longer fruiting pedicels, and from subsp. *D. a.* subsp. *rivensis* by its shorter, narrower lamina, that is especially narrower relative to width at 3/4 length, and calyx tube that is narrower relative to width as well. This subspecies is named in honor of the late John Dwyer, collector of the type specimen and renowned plant taxonomist, ethnobotanist, professor at Saint Louis University, and research associate of the Missouri Botanical Garden.

1d. Diospyros acapulcensis Kunth subsp. **guanacastensis** M.C. Provance, I. García & A.C. Sanders, subsp. nov. **(Figs. 8, 20a–b)**. TYPE: COSTA RICA. GUANACASTE: Parque Nacional Palo Verde, Sector Catalina, Camino y Sendero Botija Saliendo al Campo de aterrizaje del Refugio Palo Verde, 10°21'N, 85°21'W, 20 m, 26 Nov 1991, *U. Chavarría 427* (HOLOTYPE: MO-5700632!; ISOTYPE: INB).

Arbores a *Diospyros acapulcensi* ssp. *acapulcensi* similis sed differt fructibus fuscatis, calycibus fructiferis extus viscidissimus vestimento atroferrugineo ac rubri-aureo.

Trees 2–10 m tall; **trunk** to 30 cm in diameter, whitish to grayish-white; **stems** glabrous or with ashy remnants of hairs when mature, densely hairy when young, the hairs ascending to upright, bright reddish-orange to brownish, the epidermis shiny and viscid. **Petioles** 4–7 mm long, rugose, viscid and shiny, brick red to dark reddish-brown, densely pubescent below, the hairs bright, blond to reddish-gold, shorter above. **Lamina** chartaceous, 45–85(–95) mm long, 20–35 mm wide, length to width ratio (1.8–)2–2.8 **:** 1, oblanceolate to obovate or oblong-ovate, sometimes nearly elliptic, *base* acute to obtuse, abruptly decurrent on the petiole, *margin* flat to minutely revolute, sometimes ciliate, *apex* acute to obtuse; **lower lamina surface** ascending-pubescent, the hairs golden to ferruginous, clavate glandular hairs often present, the epidermis dark reddish-brown and sometimes black-mottled, the stomatal apparatus translucent and inconspicuous; **upper lamina surface** densely wavy-hairy, the hairs deciduous, leaving seeping annular papillae, clavate glandular hairs often present, deciduous, leaving the epidermis viscid, the epidermis dark, often tented, crystal-papillose. **Venation** eucamptodromous, viscid, prominent below, often 3-ribbed from the base; **midrib** rugulose below, densely hairy, the long ascending to spreading hairs sometimes sticking to the epidermis, midrib impressed above and wavy-hairy; **lateral veins** 6–9 per side; **3° veins** on lower surface similar to the midrib below. **Male inflorescences** 3–5-flowered cymes, partly ascending-pubescent, partly tomentulose; **peduncles** 1–2 mm long; **pedicels** 1–2 mm long, bracts lance-ovate, 1.5–2.5 mm long, navicular. **Male flowering calyx** glabrous inside except for a very narrow intramarginal band on the lobes, exterior partly wavy subappressed to ascending-pubescent, partly tomentulose, the epidermis viscid, dark brown, *tube* 3.5 mm long, 3 mm wide, sometimes vaguely keeled from the sinus to the base, *lobes* acute, 2–2.5 mm long, 2 mm wide; **male corolla tube** 6 mm long, 2 mm wide, sericeous except for 3 basal shield-shaped glabrous zones, ± 1.5 mm long, these minutely puberulent distally; **male corolla lobes** ovate to elliptic, 3 mm long, 1 mm wide. **Stamens** 12; **filaments** adnate to the base of the corolla, a few sometimes inserted on the receptacle, 1.5–2 mm long, sometimes geminate, red; **anthers** lanceolate, 2 mm long, aristate. **Female inflorescences and flowers** unknown except **styles remnants on immature fruit** columnar, hairy, 3 in number. **Fruiting pedicels** stout, 0.5–2.5(–5) mm long, fissured to shallowly grooved, sparsely to densely hairy, the hairs reddish-gold, bracts ovate to deltoid and sharply pointed, 1.2–1.6 mm long, flat to vaguely concave. **Fruiting calyx** semi-globose when immature, explanate and torn at the sinuses when mature, densely hairy outside, in part tomentulose, in partly villous, the hairs tawny to brilliant reddish-gold, ± deciduous, the epidermis dark brown, shiny and viscid, *tube* 6–10 mm long, without a bulbous base, the upper 1/2 densely hairy inside, the lower 1/2 glabrate, *lobes* obtuse, 3.5–7.5 mm long, 9.5–13 mm wide, barely acuminate to a point, usually reflexed, densely hairy inside with wide intramarginal band, the hairs

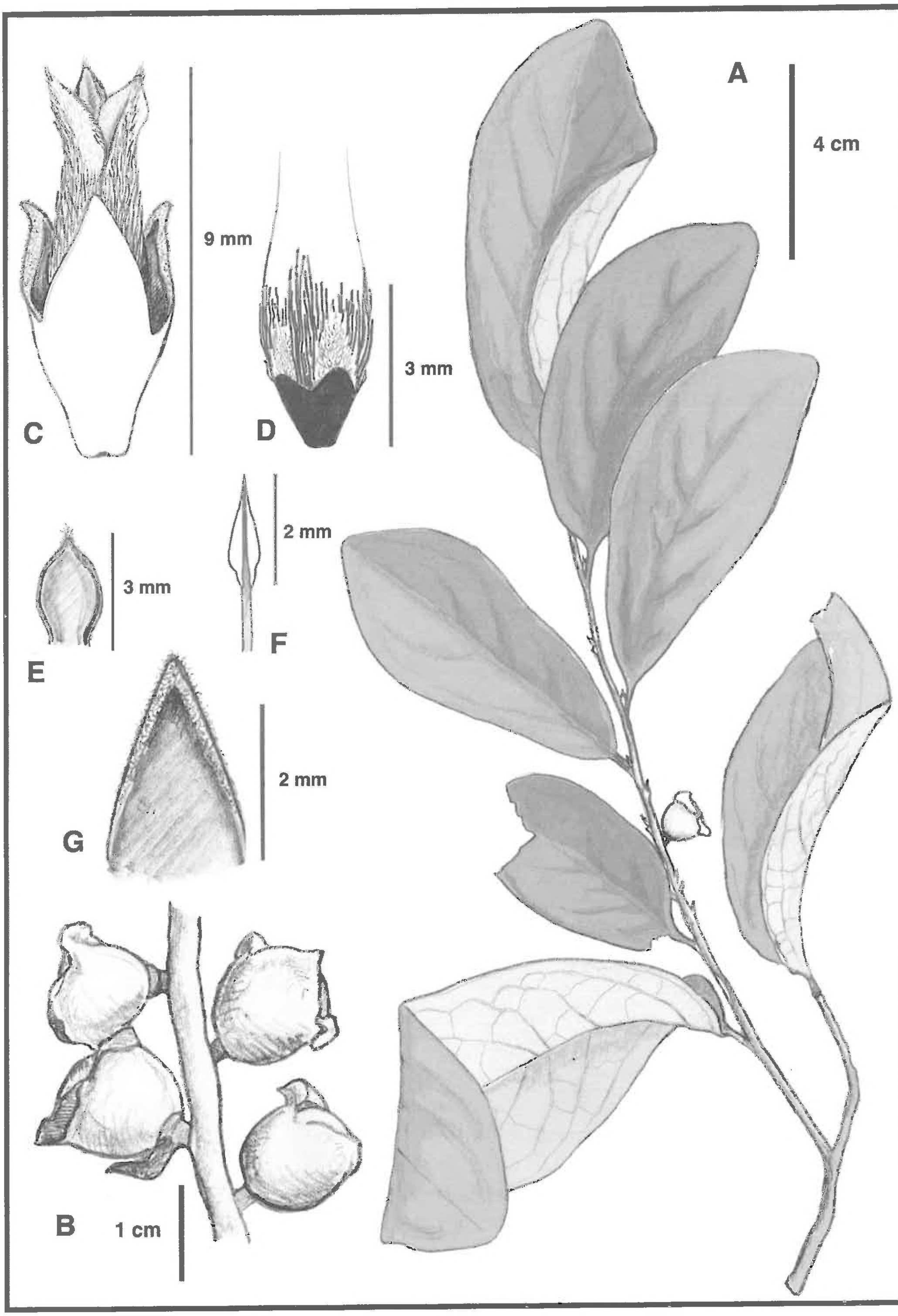

Fig. 8. *Diospyros acapulcensis* Kunth subsp. *guanacastensis* M.C. Provance, I. García & A.C. Sanders, subsp. nov. **A–B.** Based on the holotype (*U. Chavarría 427*, MO-5700632). **A.** Branchlet with calyx of immature fruit. **B.** Immature fruiting calices. **C–G.** *A.M. Brenes 15605* (BH). **C.** Male flower. **D.** Male corolla tube (proximal half). **E.** Male corolla lobe (adaxial side). **F.** Stamen. **G.** Adaxial surface of male calyx lobe.

tawny. **Fruit** 1.5–2(–2.3) cm in diameter, gold to reddish-brown ascending-velutinous until nearly mature, then glabrate, glaucous-pruinose, sometimes minutely gland-dotted, reportedly green (when mature) to orange-brown (presumably when fully ripe) in life, epidermis brownish, and sometimes quite dark, in herbarium specimens. **Seeds** 14 mm long, 6 mm radial depth, 4 mm wide.

This subspecies is geographically isolated from both *D. a.* subsp. *nicaraguensis* and *D. a.* subsp. *pedromorenoi* in Nicaragua, being endemic to dry tropical forest near sea level to 800 m in NW and central Costa Rica (Fig. 24). In NW Costa Rica it has been collected on the Nicoya Peninsula at Barra Honda National Park, the Island of San Lucas, and the southern slopes of the Cordillera de Guanacaste at Rincón de la Vieja National Park. Other sites include the vicinities of Bagaces, Cañas, and Palo Verde National Park. The NW limit of this subspecies appears to be Santa Rosa National Park. Material intermediate with *D. a.* subsp. *rivensis* has been collected on Cerro El Hacha at 1100 m. Collections from near sea level at the SE extreme of the Nicoya Peninsula, and from the margins of the Candelaria River in central Costa Rica are difficult to place, and may be intermediates with *D. a.* subsp. *rivensis*. Some specimens from the Department of Guanacaste have rather distinctive leaves and fruiting calyces (as seen in the type) that are very viscid, have a dark reddish-brown epidermis, and a brilliant reddish-gold vestiture. Annular glands on both leaf surfaces are derived from deciduous hairs that have left the basal portion of the fluid-filled trichome and/or the swollen region of the epidermis at the base of the trichome. These are particularly conspicuous in collections from Palo Verde National Park and San Lucas Island. This subspecies differs from *D. a.* subsp. *nicaraguensis* in its longer fruiting calyx tube, shorter distance between superadjacent lateral veins, intense golden to reddish-brown vestiture and dark fruits. Compared to *D. a.* subsp. *pedromorenoi*, this subspecies has smaller fruits, shorter fruiting pedicels, a longer fruiting calyx tube, and different stem, inflorescence, and abaxial lamina vestiture.

Representative specimens. **COSTA RICA. Alajuela:** entre Bagaces y Los Cañas, 29 May 1932, *A.M. Brenes 15605* (BH). **Guanacaste:** P.N. Rincón de la Vieja, 700–800 m, 16 Oct 1990, *Gerardo Rivera 780* MO); P.N. Palo Verde, 10–150 m, 9 Jan 1992, *U. Chavarría 475* (BM); near Bagaces, 50 m, 26 Apr 1972, *P.A. Opler 761* (MO); 15 km S of Liberia, 170 m, 4 Jul 1971, *W.E. Harmon & J.A. Fuentes 6068* (UMO); Hacienda La Pacifica, near Cañas, 19 Aug 1985, *D.S. Seigler DS-12401* (MO, ILL), same location, 14 Aug 1986, *D.S. Seigler DS-12782* (MO, ILL); Llanos de Cortes, 24 Jan 1984, *T.D. Pennington & L.J. Poveda 11420* (MO); P.N. Rincón de la Vieja, Est. Las Pailas, 800 m, 3 Nov 1993, *R. Espinoza 618* (MO); Santa Rosa N.P., towards Quebrada de Costa Rica, 100 m, 25 Jan 1983 *Garwood et al. 516* (MO); P.N. Santa Rosa, Bahía Salinas a Santa Cecilia, 300 m, 14 Jul 1994, *R. Espinoza 1119* (MO); Cantón de Nicoya, P.N. Barra Honda, 300—400 m, 9 Jun 1993, *Reyes 164* (MO); Est. Biol. Palo Verde, 20–90 m, 20 Dec 1992, *Quigley 931* (LSU); Tempisque, Est. Biol. Palo Verde, 10–100 m, 12 Dec 1990, *U. Chavarría 199* (MO); Ferri del Tempisque del lado de Cañas, 28 Aug 1985, *Poveda et al. 4023* (VT). **Puntarenas:** Isla San Lucas, 0 m, 29 Aug 1985, *N. Zamora V. 1087* (MO, VT); Cantón de Puntarenas Monteverde, Río Guacimal, 600-800 m, 7 Aug 1992, *W. Haber et al. 11326* (BM).

1e. Diospyros acapulcensis Kunth subsp. **mejocotensis** M.C. Provance, I. García & A.C. Sanders, subsp. nov. **(Figs. 9, 21a–b).** Type: HONDURAS. Lempira: Río Mejocote, 9 km de Gracias, [14°32'N, 88°31'W], 1000 m, 7–9 Dec 1971, *C. Nelson, M. Hernández & A. Rosales 184* (holotype: MO-4594757!; isotype: TEFH-3807!).

Arbores a *Diospyros acapulcensi* ssp. *acapulcensi* similis sed differt laminis foliorum obtrullatis latioribus, praesertim ad 3/4 longitudinem, infra viscidis atroferrugineis, fructibus paene sessilibus, et pedicellis fructiferis ebracteatis.

Trees 6 m tall; **trunk** unknown; **stems** glabrous when mature, the young stems densely hairy, the hairs mostly 0.2–0.6 mm long, slightly wavy, ascending to upright, colorless to reddish-brown, the epidermis viscid, dark reddish-brown. **Petioles** 4–6 mm long, rugose, the epidermis very viscid, golden-brown, hairy below with wavy to straight glossy hairs, these subappressed. **Lamina** chartaceous, 80–119 mm long, 35–54 mm wide (40–50 mm at 3/4 length), length to width ratio 1.9–2.5 **:** 1, obovate to obtrullate, *base* acute, decurrent on the petiole, *margin* flat, *apex* obtusely-acuminate; **lower lamina surface** densely hairy when young, the hairs curly to slightly wavy, clear to reddish-brown, glabrate when mature, the bases of the hairs slightly swollen, leaving glandular annular papillae upon loss of the hairs; **upper lamina surface** initially densely ascending wavy-hairy, also with some clavate glandular hairs, but mature leaves glabrate. **Venation** arcolanguid to eucamptodromous, the epidermis viscid, reddish-brown; **midrib** prominent below and at the base on the upper surface, vestiture similar to petiole; **lateral veins** 7–8 per side, finely raised above,

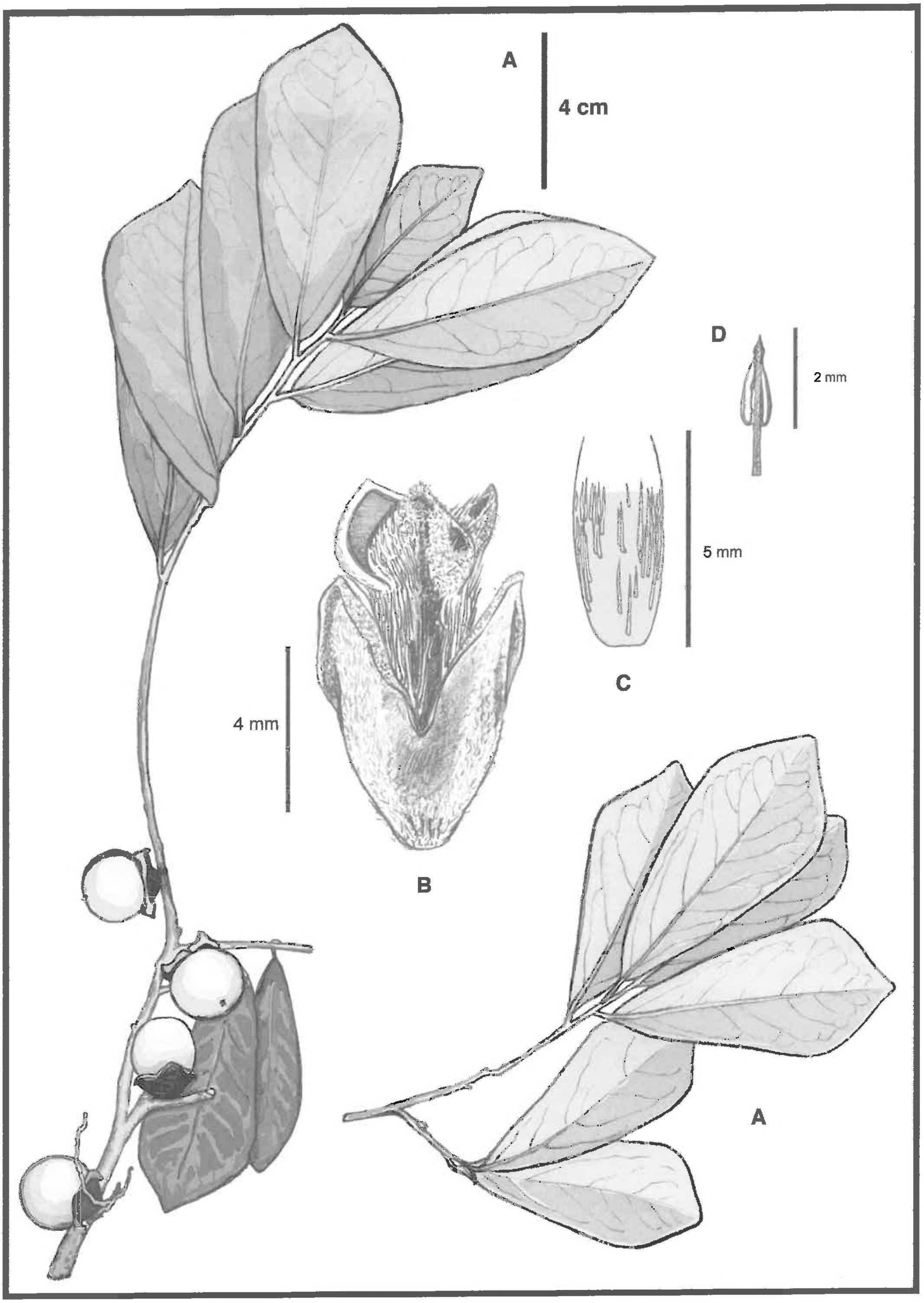

Fig. 9. *Diospyros acapulcensis* Kunth subsp. *mejocotensis* M.C. Provance, I. García & A.C. Sanders, subsp. nov. **A.** Fruiting and sterile branchlets, based on the holotype (*C. Nelson et al. 184,* MO-4594757). **B–D.** Based on *S. Blackmore & M. Chorley 3903* (TEFH). **B.** Male flower. **C.** Male corolla tube (proximal portion). **D.** Stamen.

impressed along the midrib-lamina seam; **3° venation** barely raised above and below. **Male inflorescences** 3(–6)-flowered cymes, pubescence similar to young stems; **peduncles** 2.5–4 mm long; **pedicels** 1–2 mm long, bracts 1.8 mm long, narrowly elliptic, navicular. **Male flowering calyx** glabrous inside, minutely reddish-brown kinky-hairy outside, with scattered short crooked ascending hairs, the epidermis viscid, dark reddish-brown, *tube* 3 mm long, 3 mm wide, *lobes* acute, 4 mm long, 3 mm wide, glabrate inside, with only a few straight appressed hairs near the apex and a narrow tomentulose intramarginal band, similar to the tube outside, but the hairs sparser, sometimes subappressed; **male corolla tube** 5 mm long, 2 mm wide, tawny to golden brown sericeous outside, except for 3 glabrous regions at the base, these sometimes continuing onto the petal lobe (the hairs apparently readily deciduous), the epidermis dark reddish-brown; **male corolla lobes** rhombic, strongly involute on one or both sides, 2.8 mm long, 2.8 mm wide. **Stamens** 12; **filaments** adnate to the corolla at or near the base, 1.4 mm long, dark brown; **anthers** lanceolate, 1.7–2.0 mm long, rigidly pointed, golden brown. **Female inflorescences and flowers** unknown. **Fruiting pedicels** stout, 0.3–1 mm long, bracts 0. **Fruiting calyx** campanulate, glabrate to sparsely hairy outside, sometimes with desiccated hairs stuck to the viscid, horizontally wrinkled, very dark epidermis, *tube* 7–8 mm long, base not bulbous, minutely tawny sericeous almost completely to the base, *lobes* widely obtuse, 5–6 mm long, 12–13 mm wide, vaguely acuminate to a blunt point, reflexed, tawny sericeous inside except for a broad tomentulose intramarginal band. **Fruit** globose to subglobose, 2 cm in diameter, densely subappressed golden puberulent near the apex, otherwise glabrate, epidermis glaucous-pruinose, slightly scintillant, mauve, orange-brown where the cuticular wax has been removed. **Seeds** 13 mm long, 6 mm radial depth, 3.5 mm wide.

This taxon is similar to *D. a.* subsp. *pedromorenoi*, but has nearly sessile fruit and obtrullate leaves. The fruiting calyces are similar to those of *D. a.* subsp. *veraecrucis*, but the leaves are differently shaped and have kinky to curly, upright, reddish hairs abaxially in contrast to the straight, appressed, distally-directed hairs of *D. a.* subsp. *veraecrucis*.

This subspecies has been collected twice in the Mejocote River Valley in southwestern Honduras, just E and NE of the Cordillera de Celaque (Figs. 23, 24); once in pine forests at 1000 m, and again along a tributary of the Mejocote River at about 750 m, ± 20 km NNW of this site, from "rocky cliffs over large river" (*S. Blackmore & M. Chorley 3903*). The known collections of this taxon come from places near Celaque National Park, and so it should be sought within the park boundaries along arroyos and watercourses at lower elevations.

Specimens examined. **HONDURAS. Lempira:** near Las Flores, on road Santa Rosa de Copán–Gracias [14°42'N, 88°36'W, 752 m], 13 May 1987, *S. Blackmore & M. Chorley 3903* (TEFH, BM not seen).

1f. Diospyros acapulcensis Kunth subsp. **nicaraguensis** (Standl.). M.C. Provance, I. García & A.C. Sanders, comb. et stat. nov. (**Figs. 10, 11, 18a–e**). Basionym: *Maba nicaraguensis* Standl. Contr. U.S. Natl. Herb. 20:193. 1919. *Diospyros nicaraguensis* (Standl.) Standl. Publ. Carnegie Inst. Wash. 461: 80. 1935. Type: NICARAGUA. Granada: 16 Feb 1906, *C.F. Baker 629* (holotype: US-862725 as microfiche UCSB!).

Maba nicaraguensis Standl. J. Wash. Acad. Sci. 17:526. 1927. nom. superf. Type: NICARGUA: near Managua, 16 Apr 1926, *D. Chavez 206* (holotype: US-1266111).

Trees and shrubs, 1–12(–20) m tall; **trunk** up to 30 cm in diameter, sometimes with multiple trunks, bark smooth, grayish to reddish-brown; **stems** sometimes with scant persisting hairs when mature, young stems pilose to villous, sometimes sublanate, the hairs blond to dull orange, sometimes also partly retrorse hirsutulous, with clavate glandular hairs often present, but deciduous, as a result the epidermis viscid, often mottled with black shiny regions. **Petioles** narrowly edged, (3–)3.5–6.5(–8) mm long, epidermis rugose, viscid, becoming glabrous, but initially densely hairy above and below, the hairs wavy to straight and ascending to retrorse, clavate glandular hairs often present. **Lamina** membranaceous in spring, later chartaceous, 50–120(–140) mm long, (20–)28–47(–65) mm wide, length to width ratio (1.7–)1.8–2.7(–3.3) **:** 1, elliptic to obovate-elliptic or oblanceolate-elliptic, *base* obtusely to acutely attenuate, decurrent on the petiole, *margin* flat to minutely revolute, *apex* acute to rounded, sometimes acuminate; **lower lamina surface** moderately to

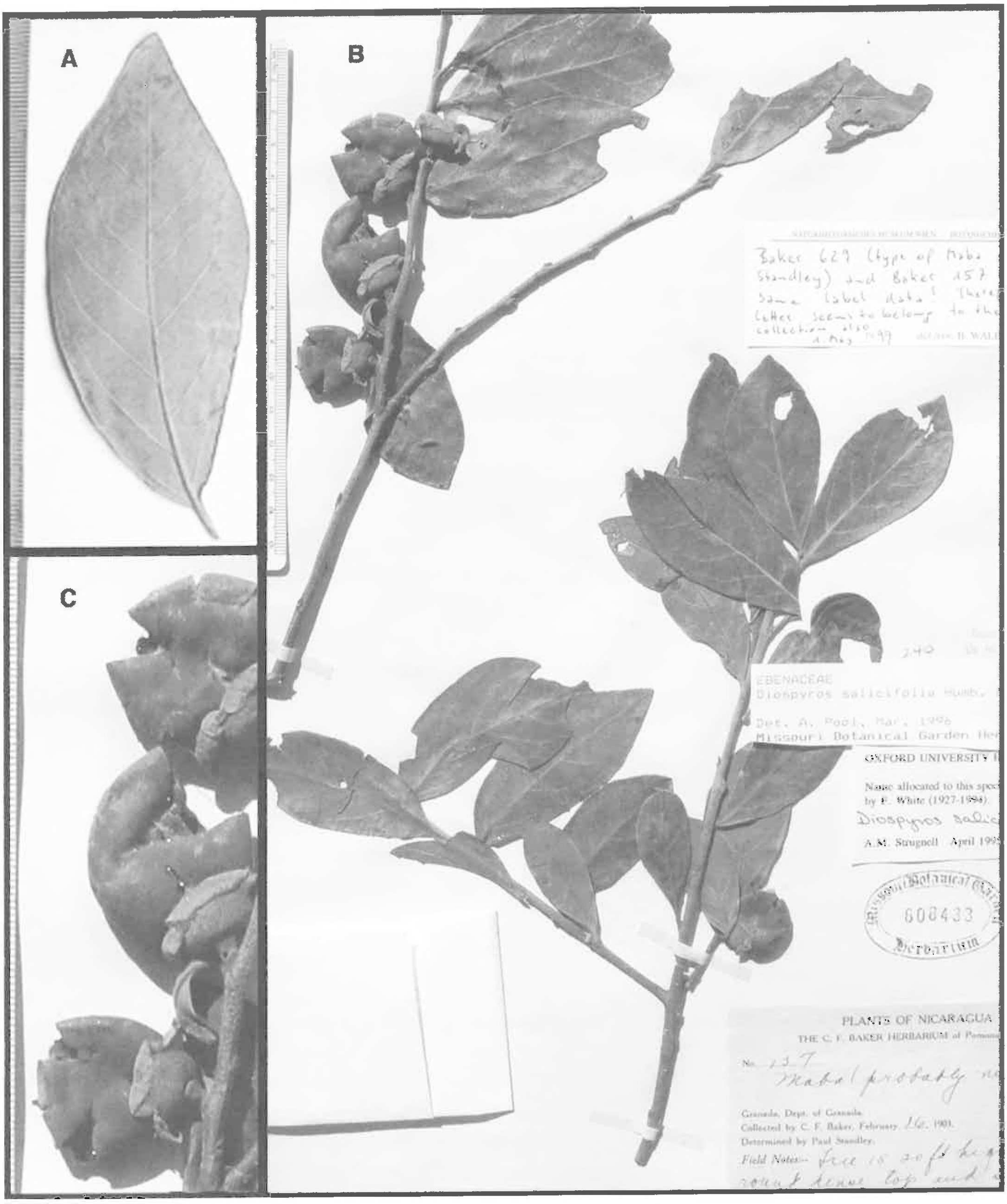

Fig. 10. *Diospyros acapulcensis* Kunth subsp. *nicaraguensis* from Granada, Dept. of Granada, Nicaragua. A. Abaxial leaf surface (*C.F. Baker 157*, ARIZ). B–C. (*C.F. Baker 157*, MO). B. Fruiting and sterile branchlets. C. Detail of fruiting branchlet.

densely hairy, the hairs straight to wavy, ascending to upright, yellowish to dull orange, clavate glandular hairs often present, but deciduous, epidermis brownish-green, the stomatal apparatus translucent to opaque, often conspicuous; **upper lamina surface** villous, clavate glandular hairs often present, but deciduous, epidermis dark grayish-green, sometimes crystal-papillose. **Venation** eucamptodromous; **midrib** prominent below, hirsute, especially along the sides, some hairs slightly wavy, hairs curly to straight above, mostly upright,

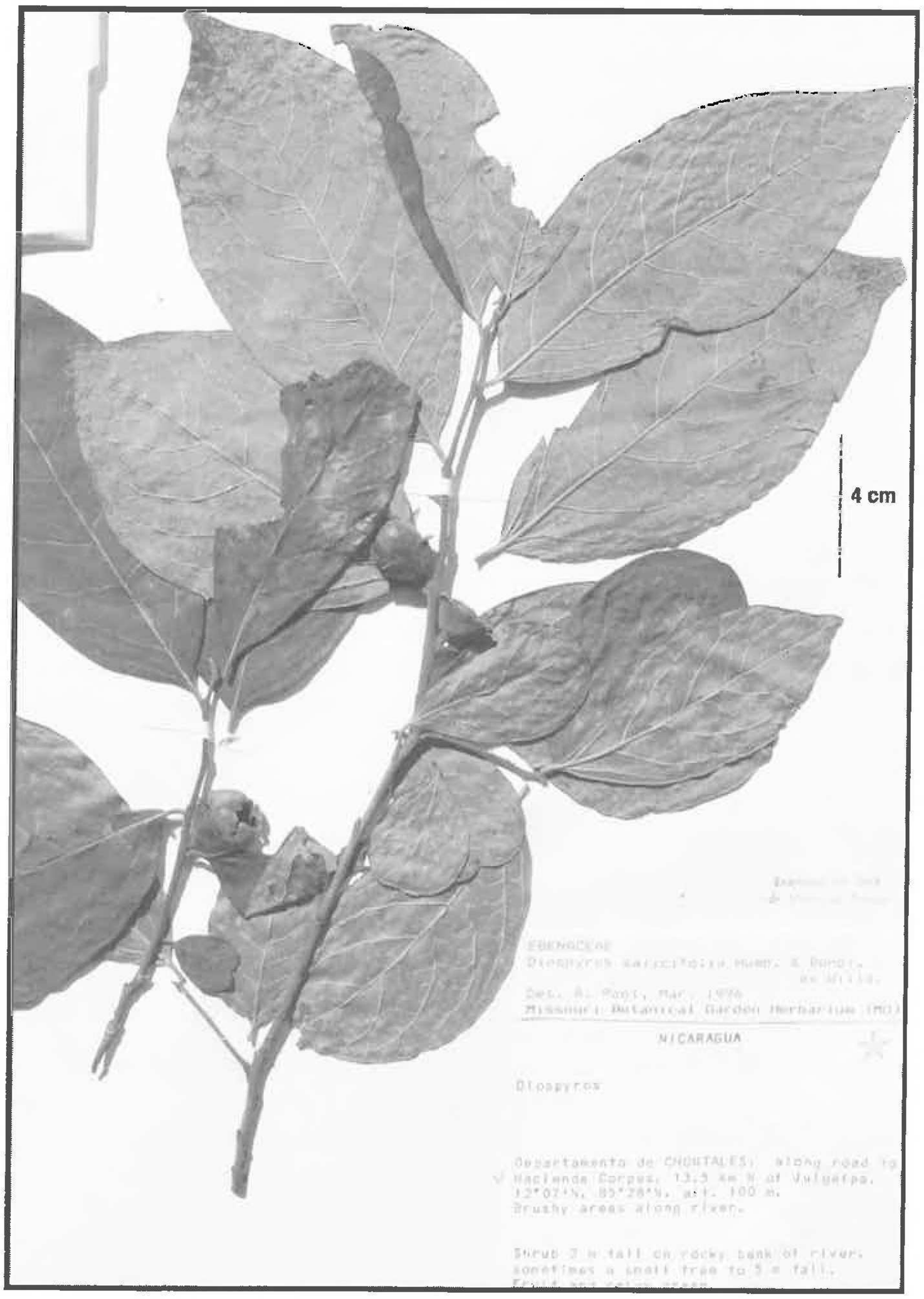

Fig. 11. ***Diospyros acapulcensis*** **subsp.** ***nicaraguensis*** **from 13.5 km W of Juigalpa, Dept. of Chontales, Nicaragua (*M. Nee 27612*, MO).**

but ascending to retrorse basally; **lateral veins** (5–)7–10(–12) per side, prominent below, raised above; **3° veins** prominent below, usually raised above; **4° veins** barely raised below, sometimes darkened in young leaves. **Male inflorescences** 1–3-flowered cymes, densely minutely wavy-hairy; **peduncles** (3–)4–6 mm long; **pedicels** 1.5–2 mm long, bracts lanceolate, 1.5 mm long. **Male flowering calyx** densely tomentulose outside, the epidermis viscid, dark brown; *tube* 2.5–4 mm long, 3–4.5 mm wide, glabrous inside, *lobes* acute, 3.5–6 mm long, 2–4 mm wide, bluntly pointed, sericeous inside except for a narrow intramarginal band; **male corolla tube** 5–7 mm long, 2–3 mm wide, cream to pinkish sericeous outside, with 3-4 shield-shaped glabrous basal regions, glabrous and sericeous areas sometimes separated by a few minute retrorse hairs; **male corolla lobes** white, cream, yellow, or red (reportedly, perhaps in error), lanceolate, ovate or rhombic, 2–4 mm long, 1–2 mm wide. **Stamens** 12; **filaments** adnate to the corolla at or near the base of the tube, sometimes inserted on the receptacle, 0.8–1.5 mm long, sometimes geminate; **anthers** lanceolate to oblong, 1.5–2 mm long, apiculate to rostrate. **Female inflorescence** densely hairy, bracts 1–2, opposite or alternate, 1.6–2.5 mm long, lanceolate to broadly ovate, acuminate, slightly concave to navicular. **Female flowering calyx** sericeous inside, except glabrous basally and lobes with a broad tomentulose intramarginal band,

densely and minutely wavy-hairy outside, *tube* cupulate, thickened, especially basally, 1.8–2 mm long, 5 mm wide, *lobes* obtuse, 5–6 mm long, 7.5–8 mm wide; **female corolla tube** 5.5 mm long, 3 mm wide, upper 1/2 sericeous outside, basal 1/2 with 3-4 shield-shaped glabrous areas, straight retrorse hairs sometimes separating the glabrous and sericeous regions; **female corolla lobes** ovate, lanceolate or rhombic, 3 mm long, 1.8–2 mm wide; **ovary** subglobose to depressed-globose, densely and minutely hairy; **styles** 3(–4), ± 1.3 mm long, partly fused, hairy; **stigmas** ± 0.8 mm long, minutely hairy; **staminodes** ± 6, adnate to base of corolla, filaments, 1.8 mm long, sterile anthers 1 mm long, lanceolate, asymmetric basally. **Fruiting pedicels** stout, (0.5–)1–5(–7) mm long, glabrate to densely hairy. **Fruiting calyx** subrotate to campanulate, densely hairy outside, sometimes glabrate, *tube* (3–)4.5–8(–9) mm long, base often bulbous, *lobes* obtuse, 3–6.5(–7.5) mm long, (7–)9–13(–16) mm wide, reflexed; **fruit** subglobose to depressed-globose, 1.5–2.5 cm in diameter, glaucous, scintillant, yellowish, orangish or light brown, living material reportedly orange when ripe. **Seeds** 14 mm long, 7 mm radial depth, 5 mm wide.

This subspecies is found from near sea level to 1500 m in a wide range of habitats, including tropical deciduous forest, semideciduous forest, and pine-oak forest, in the cordilleras of southern Nicaragua, Honduras, northeastern El Salvador, and eastern Guatemala (Figs. 23, 24). This taxon is most similar to *D. a.* subsp. *guanacastensis,* which has a longer fruiting calyx tube, and a gold to reddish-brown vestiture and dark fruits. It forms intermediates with *D. a.* subsp. *pedromorenoi* in several areas of west-central Nicaragua. Some collections from Isla Momotombito, Lake Managua, are difficult to place, and are tentatively regarded as intermediate with *D. a.* subsp. *rivensis*. The duplicates of *C.F. Baker 157* are considered isotypes by Wallnöfer (by annotation of the MO specimen in May 1999) because they "have the same label data!" However, in addition to differences in collection number, the holotype *C.F. Baker 629* (US) label reads "about dry hills," while the *C.F. Baker 157* collections (MO, ARIZ) do not. Moreover the labels are in different handwriting. Specimens of *C.F. Baker 157* (MO, ARIZ) bear Pomona College labels, while the holotype has the U.S. National Museum label. There seems to be insufficient reason to consider *C.F. Baker 157* collections isotypes.

Representative specimens. **EL SALVADOR. Morazán:** Perquín, Rio Sapo, 25 Jan 2000, *J. Monterrosa et al. 15* (MO). **San Miguel:** San Luis Reina, 9 Jan 1975, *J.R. Martinez 315* (TEFH). **GUATEMALA. Chiquimula:** Caracol Mountain, 1.5 mi N of Quezaltepeque, 1200–1400 m, 7 Nov 1939, *J.A. Steyermark 31396* (F). **Zacapa:** above Teculután, 250–275 m, 7 Jan 1942, *J.A. Steyermark 42132* (F). **HONDURAS. Choluteca:** Tatumbla, 25 km de la capital, 1500 m, 28 Sep 1982, *V.M. Pineda s.n.* (MO). **Comayagua:** Chichipates, *C. Nelson et al. 6746* (TEFH). **Cortés:** orilla del Río Humuya, 40 km N Santa Cruz de Yojoa, 100 m, 1–30 Nov 1980, *C. Nelson et al. 5752* (TEFH, MO). **El Paraíso:** near Casitas, 900 m, 4 Dec 1946, *L.O. Williams & A. Molina R. 11074* (MO). **Francisco Morazán:** slopes on Cerro Majicarán, 900 m, 14 Jun 1947, *A. Molina R. 108* (MO). **Intibuca:** Quebrada Los Naranjos, Aldea San Juan, Magdalena, 10 Jan 1975, *J.R. Martinez 347* (TEFH). **La Paz:** between Galeras and Lizapa Grande, 1000 m, 24 Jun 1947, *A. Molina R. 167* (MO). **NICARAGUA. Boaco:** Sierra El Espino, 500–600 m, 11 Nov 1982, *P. Moreno 18526* (MO). **Carazo:** La Boquita, 13 Jul 1982, *R. Kral 69373* (MO). **Chinandega:** Faldas del Volcán Casita, 23 Jul 1982, *M. Araquistain 2982* (MO). **Chontales:** 13.5 km W of Juigalpa, 100 m, 28 Aug 1983, *M. Nee 27612* (MO); 14 km SSW of Comalapa, 150 m, 28 Aug 1983, *M. Nee 27619* (MO). **Estelí:** vicinity of Guava, 20 km of Estelí, 900 m, 5 Nov 1968, *A. Molina R. 23121* (MO). **Granada:** Granada, 16 Feb 1903, *C. F. Baker 157.* **Jinotega:** "El Eden," 7 km a la entrada del camino viejo a Jinotega, 840–860 m, 25 Oct 1983, *S. Vega & W. Robleto 99* (MO, TEFH). **Leon:** Santa Rosa del Peñón, 500–600 m, 11 Sep 1980, *P. Moreno 2440* (MO). **Madriz:** Cerro Quisica, 800–1100 m, 23 Nov 1979, *W.D. Stevens 16181* (MO). **Managua:** El Tamrindo, ± 300 m, 1 Dec 1983, *P. Moreno 22524* (MO); entrada a la hacienda San Ramón, 18 Oct 1982, *P. Moreno* 17919 (MO). **Masaya:** Laguna de Apoyo, 100–140 m, 20 Sep 1981, *P. Moreno 11140* (MO). **Matagalpa:** El Caao–Caserio Puertas Viejas, 460 m, 25 Aug 1983, *J.S. Miller 1286* (MO). **Nueva Segovia:** 6 km N of Ocotal, 700 m, 15 Jun 1977, *D. Neill 2145* (MO).

1g. Diospyros acapulcensis Kunth subsp. **pedromorenoi** M.C. Provance, I. García & A.C. Sanders, subsp. nov. (**Figs. 12, 20c–d**). Type: NICARAGUA. Estelí: San Juan de Limay, Valle San Juan de Tranquera, entre San Juan de Limay y Pueblo Nuevo, 13°15'N, 86°35'W, 400–450 m, 5 Sep 1980, *P. Moreno 2386* (holotype: MO-3307430!).

Arbores et frutices a *Diospyros acapulcensi* ssp. *acapulcensi* similis sed differt petiolis longioribus rugulatis malvinus vel purpureus glauco-pruinosis, laminis foliorum supra dense vestitis trichomatibus crispulatis ferrugineus ac costis latioribus, et fructibus majoribus (usque ad 3.5 cm diam.).

Trees, rarely shrubs, 2–12 m tall; **trunk** unknown; **stems** glabrous to densely hairy when mature, the hairs wavy, ascending, dull orange to golden-brown, becoming desiccated and ashy, those of young stems sometimes mixed with sparse longer, wavy, spreading to ascending hairs, with clavate glandular hairs often present, but deciduous and leaving the brown to dark brown epidermis viscid. **Petioles** 4–7 mm long, densely tomentulose

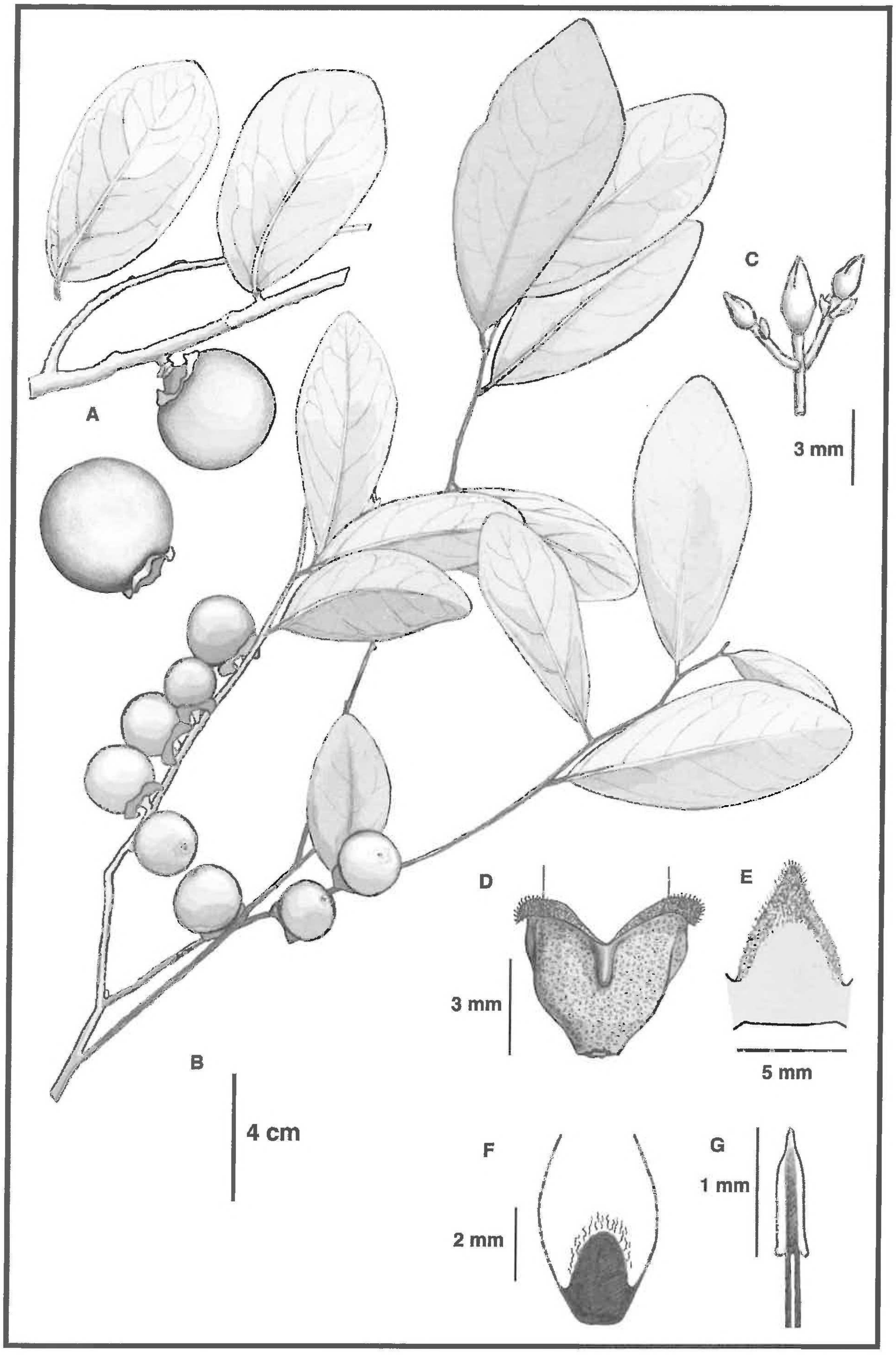

FIG. 12. *Diospyros acapulcensis* Kunth subsp. *pedromorenoi* M.C. Provance, I. García & A.C. Sanders, subsp. nov. **A.** Fruiting branchlet with loose leaf and fruit from Los Cerritos, Dept. of Estelí, Nicaragua (*P. Moreno 10887,* MO). **B.** Fruiting branchlet, based on the holotype from Valle San Juan de Tranquera, Dept. of Estelí, Nicaragua (*P. Moreno 2386,* MO-3307430). **C–G.** Based on *P. Moreno 21526* (MO) from Hacienda San Antonio, Dept. of Boaco, Nicaragua. **C.** Male inflorescence. **D.** Male calyx. **E.** Adaxial surface of male calyx. **F.** Diagram of proximal region of male corolla tube. **G.** Stamen.

or with short golden-brown wavy hairs, but soon glabrous, rugose, glaucous-pruinose, mauve to dark purple, reddish-brown and shiny where rubbed, clavate glandular hairs sometimes present on the upper surface. **Lamina** chartaceous, 60–122 mm long, 25–60 mm wide, length to width ratio (1.8–)2–3(–3.3) **:** 1, broadly obovate, oblanceolate or elliptic, *base* short-attenuate, *margin* often slightly revolute, *apex* subacute to obtuse or rounded, sometimes slightly acuminate or tapering abruptly; **lower lamina surface** densely hairy, the hairs short and curly to wavy, golden to reddish-brown, clavate glandular hairs often present, deciduous, leaving the reddish-brown epidermis viscid, the stomatal apparatus translucent and inconspicuous; **upper lamina surface** glabrate to ascending wavy-hairy, deciduous, clavate glandular hairs often present, but deciduous, the epidermis viscid, dark greenish-brown, papillate or sometimes crystal-papillose,. **Venation** eucamptodromous, usually 3–5-ribbed; **midrib** prominent below, conspicuously wide, hairs denser on the midrib than on the lamina, lower midrib glaucous-pruinose, shiny, reddish-brown; **lateral veins** 6–9 per side, very prominent to subcylindrical below, slightly raised above; **3° veins** prominent below; **4–5° veins** often darkened below. **Male inflorescences** 3–5(–6)-flowered cymes, densely buff to dull orange with wavy hairs; **peduncles** 4–6 mm long; **pedicels** 1–3 mm long, bracts lanceolate, 1–1.6 mm long, conduplicate. **Male flowering calyx** densely clear to light gold minute wavy-hairy outside, with clavate glandular hairs often present, deciduous, epidermis reddish-brown, *tube* 2.0–3.5 mm long, ± 3 mm wide, glabrous inside, *lobes* lance-ovate to ovate, 3.0–5.5 mm long, 2–3 mm wide, barely winged or not, acute to acuminate, glabrous to sparsely hairy inside with a narrow tomentulose intramarginal band, sometimes with sparse clavate glandular hairs present; **male corolla tube** 3.2–5.5 mm long, ± 2.5 mm wide, white sericeous outside with 3 small basal shield-shaped glabrous areas; **male corolla lobes** oblong-ovate, 2.5–3 mm long, ± 1.8 mm wide. **Stamens** 12; **filaments** adnate to the corolla in two 6-stamen tiers, the inner basal, the outer just above, ± 1 mm long, dark reddish-brown. **Female inflorescence and flowers** unknown except **style remnants on immature fruit** fused into a hairy column, 3 in number. **Fruiting pedicels** stout, 2–4 mm long, densely hairy, with clavate glandular hairs sometimes present, epidermis reddish-brown, bracts (0–)2, opposite, often immediately subtending the fruit, broadly ovate, 1.8–1.9 mm long, flat. **Fruiting calyx** campanulate to infundibuliform, densely minutely kinky to curly-hairy outside, the hairs, orangish to reddish-brown, clavate glandular hairs sometimes present, but deciduous, leaving the reddish-brown epidermis viscid, *tube* 5–7(–8) mm long, glabrous inside basally, *lobes* obtuse to acute, 4.5–6 mm long, (9–)12–15 mm wide, abruptly acuminate to a blunt point, margins often reflexed, golden to reddish sericeous inside except for a wide tomentulose intramarginal band. **Fruit** up to 3.5 cm in diameter, glabrous to scantily hairy, glaucous-pruinose, dull yellow, mauve or purplish, often reddish-brown where rubbed, yellow to orange in life. **Seeds** 14–16 mm long, 6–7 mm radial depth, 5–6 mm wide.

This subspecies is notable for leaves with a broad, viscid, reddish-brown abaxial midrib, dense with curly to kinked reddish-brown hairs, rugose mauve to purple glaucous-pruinose petioles, and large fruit that are second in size only to *D.* aff. *inconstans* for the complex in Mesoamerica. It seems to be endemic to Nicaragua (Fig. 24), with most collections from gallery forests and rocky slopes of west-central Nicaragua. It forms intermediates with *D. a.* subsp. *nicaraguensis* in several areas. The fruit is known locally as 'chocollo,' 'chochoyo' or 'chocoyito' and is eaten when mature. This subspecies is named in honor of Pedro P. Moreno, the collector of the type, and an expert on the flora of Nicaragua.

Specimens examined. **NICARAGUA. Boaco:** Hacienda San Antonio, 200 m, 14 Jun 1983, *P. Moreno 21526* (MO); 1 km N of San José de Los Remates, 650 m, 27 Jul 1983, *W.D. Stevens & P. Moreno 22297* (MO); **Chontales:** ca. 13.1 km N of Hwy 7 on road to Cuapa, ca. 155 m, 15 Feb 1978, *Pipoly 2029* (MSC); same location and date, *W.D. Stevens 6493* (MO); Hacienda Veracruz, 120–475 m, 17 Jul 1983, *Stevens 22256* (MO), same location, 4–6 Aug 1983, *W.D. Stevens 22368* (MO); 8 km S of Cuapa, 200–375 m, 21 Sep 1983, *M. Nee 28260* (MO). **Estelí:** Salto de Estanzuela, 1000 m, 10 Sep 1980, *M. Guzmán et al. 1162* (MO); Llano Gualilica, 280 m, 2 Sep 1980, *P. Moreno 2091* (MO); Paso León, 800–820 m, 29 Mar 1983, *P. Moreno 21063A* (MO); Los Cerritos, 860–900 m, 13 Sep 1981, *P. Moreno 10887* (MO); Portal de Belén, 660–800 m, 1 Aug 1983, *P. Moreno 21845* (MO); Cerro Cucamonga, Río Waswalí, 800–850 m, 3 Jan 1982, *P. Moreno 14119* (MO); Res. Nat. Miraflor, 600–850 m, 23 Dec 1999, *R. Rueda et al. 12568* (MO); 0.5 km S de San Juan de Limay, 250–300 m, 3 Sep 1980, *P. Moreno 2236* (MO); Llano el Pozo, 1200–1300 m, 26 Dec 1982, *P. Moreno 19345* (MO); 'Hacienda La Grecia,' 518 m, 2 Sep 1980, *P. Moreno 2173* (MO) *& 2134* (MO); Las Cuevas, 1000–1100 m, 1 Feb 1983, *P. Moreno 19918* (MO); along road to Yalí, 820–1100 m, 14 Nov 1979, *W. Stevens & A. Grijalva 15508* (MO). **Leon:** Hacienda Las Lajas, 300–350 m, 4 Sep 1980, *P. Moreno* 2295 (MO); Malpaísillo,

faldas del Cerro Negro, 100–200 m, 8 May 1984, *M. Castro 122* (MO); La Chibola, 28 Jun 1984, *M. Castro 143* (MO); Llano San Lorenzo, 250–300 m, 4 Sep 1980, *P. Moreno 2327* (MO). **Managua:** camino entre "Puertas Viejas" y "Santa Juana," ± 100–120 m, 1 Jul 1983, *M. Araquistain 3584* (MO). **Matagalpa:** 3 km al E de Puertas Viejas, 400–500 m, 10 Feb 1983, *P. Moreno 20105 & 20090* (MO); camino de "Puertas Viejas," 500–600 m, 21 Sep 1983, *M. Araquistain 3668* (MO, BH); ca 5 km al NW de la ciudad de Matagalpa, 22 Jul 1983, *A. Grijalva & F. Ortiz 2825* (MO).

1h. **Diospyros acapulcensis** Kunth subsp. **rivensis** M.C. Provance, I. García & A.C. Sanders, subsp. nov. (**Figs. 13, 14, 15, 17a–i, 21d, 22a–b**).

Type: NICARAGUA. Rivas: Isle Ometepe, Volcán Concepción, camino de "Los Hatillos" a "Altagracia," 11°34'N, 85°35–39°W, 133–150 m, 13 Aug 1984, *W. Robleto 1088* (holotype: MO-3508354!; isotype: TEFH!).

Arbores et frutices a *Diospyros acapulcensi* ssp. *acapulcensi* similis sed differt laminis foliorum plerumque longioribus ellipticioribus infra strigosis trichomatibus rectis adpressibus vel subadpressibus apicem versus, supra saepe onustis fasciculis parvis crystallis albis opacis secus venas impariter projectis, et calycibus fructiferis lobis angustioribus.

Trees or shrubs 2–10 m tall; **trunk** unknown; **stems** moderately to densely velutinous when young, the hairs tawny to reddish-brown, slightly wavy or curved, subappressed, sometimes also minutely hirtellous, glabrous or only sparingly hairy when mature, the remnant hairs shorter, curved, and more upright, clavate glandular hairs often present, the epidermis sometimes very dark. **Petioles** sometimes winged, much broader than thick, 4–8 mm long, epidermis relatively smooth, yellowish to brownish, shiny and viscid, lower surface glabrate to velutinous, the hairs appressed to subappressed, straight to slightly wavy, upper surface somewhat flattened to slightly canaliculate, puberulent, the hairs appressed to upright. **Lamina** chartaceous to subcoriaceous when mature, 70–130(–150) mm long, 25–50 mm wide, length to width ratio (2.1–)2.5–3.5(–3.8) : 1, widely obovate to narrowly oblanceolate or elliptic, often crystal-papillose, *base* cuneate to acutely short-attenuate, decurrent on the petiole, *margin* slightly thickened to revolute, sometimes darkened, *apex* slightly acuminate to rounded; **lower lamina surface** velutinous to subsericeous, the hairs usually straight, but also curved, appressed and subappressed, cream to tan, clavate glandular hairs often present, the epidermis chartreuse to olive or brownish-green, sometimes papillose, the stomatal apparatus obscure; **upper lamina surface** often tented, sparsely to moderately hairy, the hairs straight or curved, appressed to ascending, sometimes deciduous, especially near the midrib, sometimes leaving a seeping ring-like gland, epidermis light greenish-brown to brownish-green, shiny. **Venation** arcolanguid, sometimes 3-ribbed; **midrib** prominent below, subsericeous, the hairs curved to nearly straight, subappressed to upright, thickish, tawny to golden-brown, clavate glandular hairs often present, but deciduous and leaving the yellowish to reddish-brown epidermis viscidulous, midrib slightly impressed to raised above, impressed along the lamina-midrib seam, pubescent, the hairs wavy to curved, ± upright; **lateral veins** (5–)6–9(–12) per side, prominent below, raised above; **3° veins** slightly raised to prominent below, barely raised above. **Male inflorescences** 3–5(–6)-flowered cymes, densely pubescent, the hairs kinky, curved, or wavy, cream, epidermis brown; **peduncles** 4–6 mm long; **pedicels** 2–3 mm long, bracts ovate to oblong-ovate, or deltoid. **Male flowering calyx** moderately to densely hairy outside, the hairs variously straight, wavy, or curly, cream to tawny, the epidermis orangish-brown to reddish, sometimes quite dark, *tube* 2.5–4 mm long, 3–3.2 mm wide, glabrous inside, *lobes* acute, 1.8–4 mm long, 1.5–3 mm wide, glabrous inside, except for a narrow tomentulose intramarginal band, and some scattered appressed wavy hairs on the median; **male corolla tube** 4–5 mm long, 2–4 mm wide, cream, tawny, yellowish or reddish-pink sericeous outside except for 3 basal shield-shaped glabrous zones; **male corolla lobes** reportedly cream to silvery and pearlescent in life, lanceolate to ovate or oblong, ± 3.5 mm long, 1–2 mm wide. **Stamens** 12–14; **filaments** partly adnate to corolla base, partly inserted on the receptacle, 1.2–1.5 mm long, rarely geminate, dark reddish-brown; **anthers** lanceolate to ovate or oblong-ovate, 1.1–2 mm long, yellowish, nearly cylindrical prior to opening, apex long-acuminate to blunt. **Female inflorescences and flowers** unknown. **Fruiting pedicels** 0.5–9 mm long, minutely hairy, often coated with exudate, bracts lanceolate to ovate, 1–2 mm long, navicular. **Fruiting calyx** spreading to crateriform (in the widespread form) or campanulate to vaguely infundibuliform (in the pale-leaved form), usually splitting below the sinuses, minutely sericeous to tomentulose outside, clavate glandular hairs sometimes present, the epidermis viscid, sometimes dark brown, sometimes black gland-dotted, *tube* 4–7.5 mm long, upper 1/2–3/4 sericeous inside, the lower 1/2–1/4 glabrate, sometimes

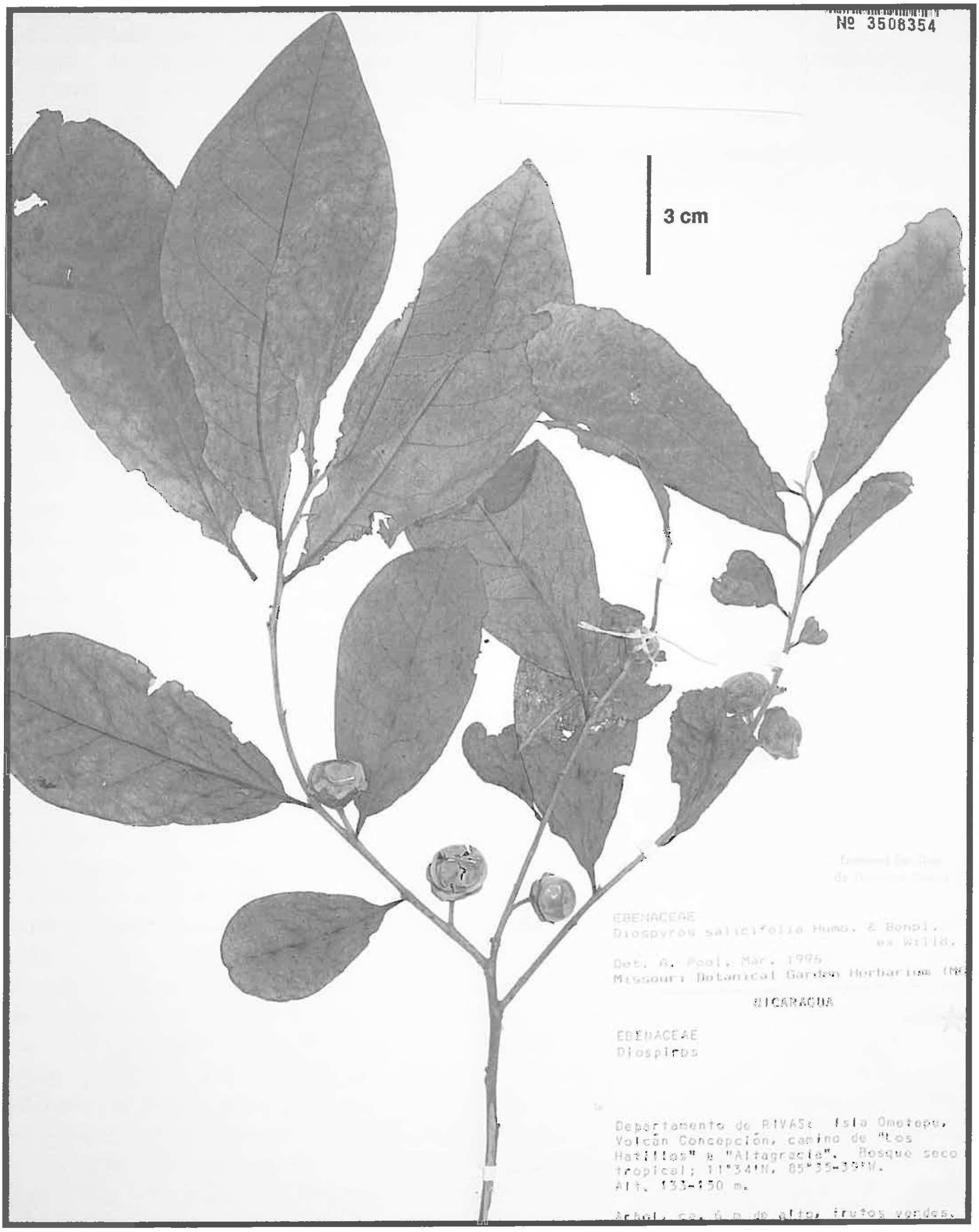

Fig. 13. Holotype of *D. acapulcensis* Kunth subsp. *rivensis* M.C. Provance, I. García & A.C. Sanders, subsp. nov. from Volcán Concepción, Isle Ometepe, Dept. of Rivas, Nicaragua (*W. Robleto 1088*, MO-3508354).

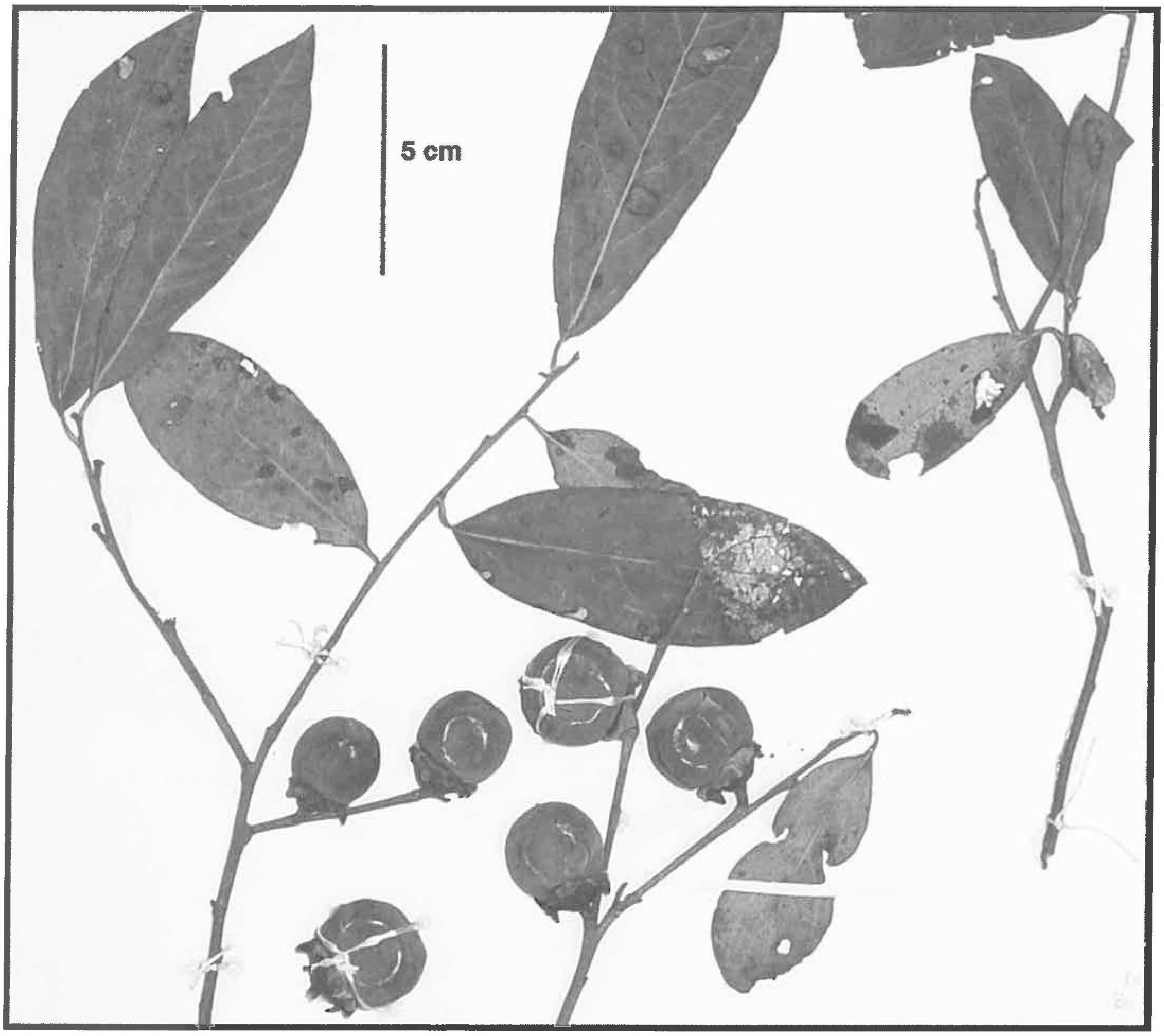

Fig. 14. Pale-leaved form of *D. acapulcensis* Kunth subsp. *rivensis* M.C. Provance, I. García & A.C. Sanders, subsp. nov. from Laguna de Apoyo, Dept. of Masaya, Nicaragua (*P. Moreno & J.C. Sandino 6185,* MO-3307419).

with scattered, thick, cylindrical glands, *lobes* obtuse, (2.5–)3.5–7 mm long, 9–15 mm wide, spreading to strongly reflexed, the apex often folded to an acute point, cream to tan sericeous inside except for a tomentulose intramarginal band. **Fruit** 2–2.6(–3) cm in diameter, glabrate, sometimes minutely hairy, tawny hairs present at the apex, epidermis sometimes minutely red to black gland-dotted, usually glaucous-pruinose, sometimes scintillant, dull yellow to brownish-orange or mauve, reportedly yellow or orange when mature, and orange to red when ripe. **Seeds** 12–13 mm long, 5.5–7 mm radial depth, 4–5 mm wide.

This subspecies is found near and along the west coast of Nicaragua and northwest coast of Costa Rica, as well as on the islands of Zapatera and Ometepe in Lake Nicaragua, Nicaragua (Fig. 24). It is mainly found between sea level and 150 m in tropical deciduous forest near shorelines and along riverbanks, and sometimes in marshy areas. There are also some mid-elevation occurrences around 700 m associated with volcanic slopes. Specimens from the area between Lake Managua and Lake Nicaragua represent a form with pale abaxial leaf surfaces (Figs. 14, 15, 17a–e, 21d) found in dry tropical forest and secondary matorral between 100 and 350 m elevation. These pale-leaved plants also vary subtly in some characteristics of stem and leaf vestiture from collections of the subspecies made elsewhere, and seem to have a different fruiting

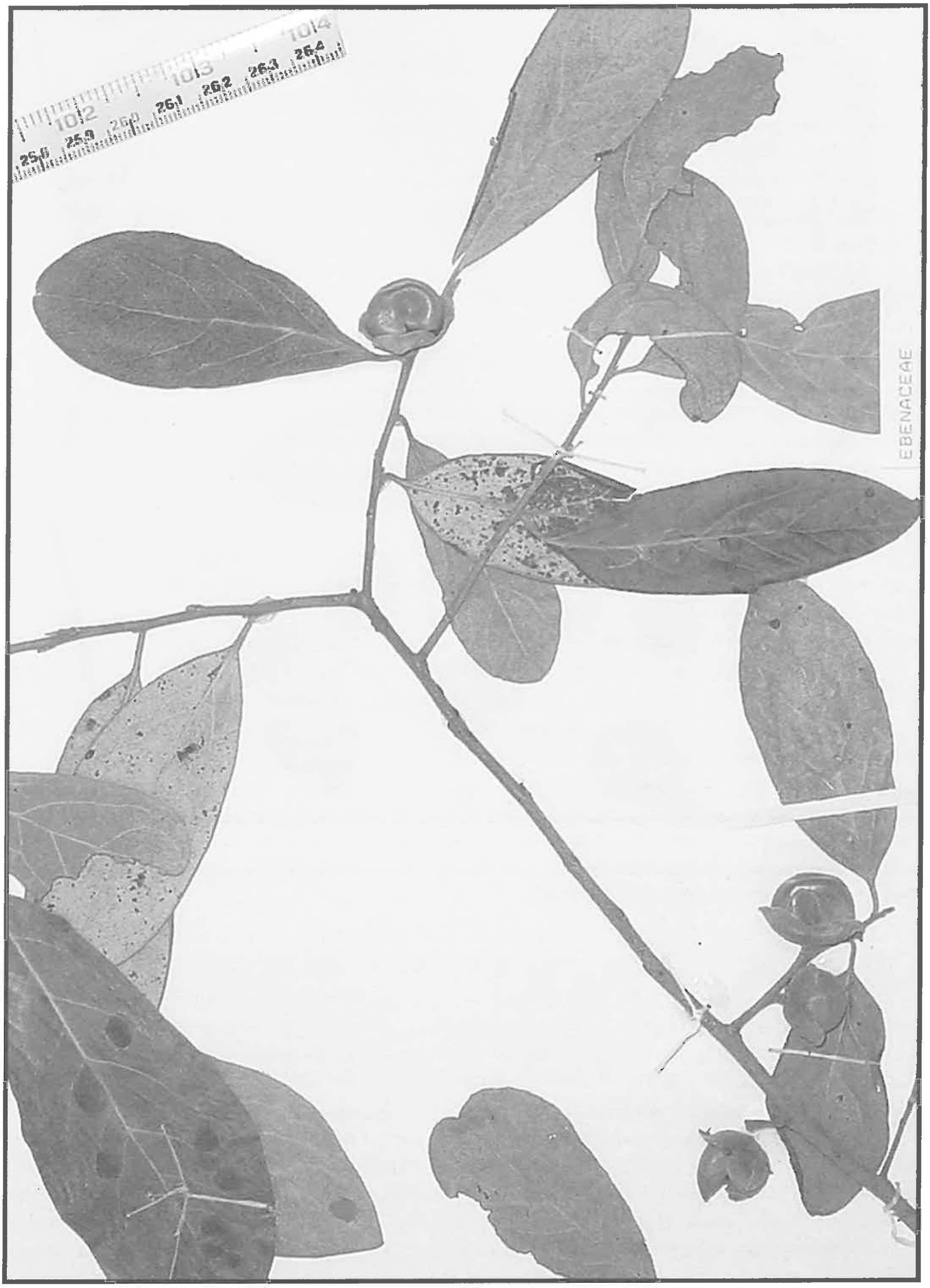

Fig. 15. Pale-leaved form of *D. acapulcensis* subsp. *rivensis* from Costado S de Lomas de Villa Fontana, Dept. of Managua, Nicaragua (*A. Grijalva 775*, MO).

calyx shape. However, the forms are indistinguishable following quantitative comparison of their vegetative and fruiting inflorescence characters. Currently, we consider plants from the area between Lake Managua and Lake Nicaragua to represent an interesting ecological variant.

Specimens that represent intergrades with *D. a.* subsp. *nicaraguensis* occur on the Island of Momotombito in Lake Managua, with *D. a.* subsp. *veraecrucis* on the volcanic Isla de la Tigre off the southern coast of Honduras, and with *D. a.* subsp. *guanacastensis* in Costa Rica. A combination of characters distinguishes this subspecies from others, including a tented lamina, straight to slightly curved, appressed to subappressed hairs on the abaxial lamina and midrib surfaces, and clusters of opaque white excrescences on the lower lamina surface. This subspecies sometimes resembles *D. a.* subsp. *veraecrucis*, but the lamina of *D. a.* subsp. *rivensis* is more elliptic, and the leaf apex more rounded. In *D. a.* subsp. *rivensis*, hairs on the lower lamina and midrib surfaces are not as straight and strongly appressed as in *D. a.* subsp. *veraecrucis*. Also petioles of this taxon tend to be longer and thinner, and the fruiting calyx lobes narrower than in *D. a.* subsp. *veraecrucis*.

Diospyros a. subsp. *rivensis* tends to have an elliptic leaf. This accounts for significant differences in several lamina shape parameters between this taxon and *D. a.* subsp. *nicaraguensis* and *D. a.* subsp. *guanacastensis*. Lamina width is also significantly narrower in *D. a.* subsp. *rivensis* than in *D. a.* subsp. *nicaraguensis*. Venation is significantly different between *D. a.* subsp. *rivensis* and *D. a.* subsp. *guanacastensis*.

This taxon has been collected in a number of protected areas, such as Santa Rosa National Park on the Santa Elena Peninsula in northwestern Costa Rica, and in Nicaragua at Reserva Natural Lagunetas de Mecatepe, Parque Nacional Volcán Masaya, Zapatera Archipelago National Park, and in Cosigüina Volcano Natural Reserve. The fruit is described as pale orange to red and sweet in late February to May. The local name 'chocoyito' appears on collections of the pale-leaved form from the area between Lake Managua and Lake Nicaragua, and on collections from the Department of Chinandega, and the islands of Zapatera and Ometepe on Lake Nicaragua. The subspecific epithet refers to the Department of Rivas, where the holotype was collected.

Specimens examined (except pale-leaved form). **COSTA RICA. Guanacaste:** P.N. Santa Rosa, Península de Santa Elena, 50–150 m, 18 Aug 1994, *B. Hammel & C. Cano 19581* (K); P.N. Santa Rosa, Península de Santa Elena, 50 m, 15 May 1993, *Carolina Cano 85* (MO); P.N. Santa Rosa, Península de Santa Elena, 3 Dec 1993, *R. Espinoza 991* (MO); P.N. Santa Rosa, Península de Santa Elena, 30 m, 30 Jul 1996, *J.F. Morales & A. Soto 5567* (MO). **Puntarenas:** Cantón de Garabito, Punta Agujas, 0–5 m, 19 Sep 1996, *J.F. Morales 5832* (K). **NICARAGUA. Chinandega:** Res. Nat. Cosigüina, Los Placeres, 0–600 m [± 37 m], 27 Mar 2001, *R. Rueda et al. 15977* (MO). **Granada:** faldas del Volcán Mombacho, bordeando la Laguna de Juan Tallo, 65 m, 23 Jul 1980, *M. Guzmán et al. 549* (MO); Isla Zapatera, Ensenada y Finca Sonzapote, 40–60 m, 20 Jan 1982, *J.C. Sandino 1910* (MO); Isla Zapatera, sobre el camino a Sonzapote, 40–55 m, 20 Jan 1982, *J.C. Sandino 1877* (MO); Isla Zapatera, entre Finca Sonzapote y Ladera NE de El Cerro, 100–300 m, *J.C. Sandino 2056* (MO); Isla Zapatera, Cerro El Llano, ca. 100 m, 13 Aug 1982, *A. Grijalva 804* (MO); Isla de Zapatera, punta al N de Finca La Habana, 30–40 m, 24 Jan 1982, *J.C. Sandino 2105* (MO); Isla Zapatera, costada NE de Hacienda Santa Maria, ± 100 m, 22 Nov 1982, *A. Grijalva 1892* (MO, TEFH). **Managua:** El Paraguay, km 26, carr. a San Rafael del Sur, 700 m, 9 Jun 1983, *P. Moreno 21466* (MO); Finca Armenia, 600 m, 2 Oct 1982, *A. & M.V. Grijalva 1330* (MO); Volcán de Chiltepe, 100–200 m, 2 Jun 1981, *P. Moreno & J. Henrich 8947* (MO); S slope and rim of Apoyeque, 220–350 m, 18 Nov 1980, *W.D. Stevens & P. Moreno 18448* (MO); "La Amistad," a 7 km de La Concha, carr. a San Rafael del Sur, 550–600 m, 11 Dec 1980, *P. Moreno 5261* (MO). **Masaya:** P.N. Volcán Masaya, lava flow N of Volcán Masaya, 250 m, 29 Nov 1977, *D. Neill 3036* (MO); P.N. Volcán Masaya, NW side of El Comalito, 285 m, 8 Feb 1978, *J.J. Pipoly 1732* (MSC); same location and date, *W.D. Stevens 6256* (MO). **Rivas:** "El Pegón," al SE de Rivas, 50 m, 21 Jan 1981, *P. Moreno 6109* (MO); convergence of Río La Pita and Río Escalante, 20 m, 3 Aug 1978, *W.D. Stevens 9692* (MO); Isla Ometepe, Volcán Maderas, ± 45 m, 16 Jun 1984, *W. Robleto 895* (MO); Isla Ometepe, Volcán Maderas, sitio "Las Cuchillas," 400 m, 14 Jun 1984, *W. Robleto 829* (MO); Isla de Ometepe, playa de Finca Santa Cruz y el Istmo de Istián, 17 Jul 1981, *J.C. Sandino 965* (MO); Isla de Ometepe, N shore of isthmus, near Santa Cruz, 25 Feb 1978, *J.J. Pipoly 2110* (MSC); same date and location, *W.D. Stevens 6623* (MO); Isla Ometepe, Volcán Concepción, 50–80 m, 28 Oct 1984, *W. Robleto 1444* (MO, TEFH); Isla Ometepe, 40–55 m, 14 Sep 1983, *P. Moreno 22040* (MO).

Specimens of pale-leaved form of *D. acapulcensis* subsp. *rivensis* examined: **NICARAGUA. Granada:** Laguna de Apoyo, 110–180 m, *P. Moreno 11174* (MO). **Managua:** Costado S de Lomas de Villa Fontana, ± 250 m, 6 Aug 1982, *A. Grijalva 775* (MO, TEFH); Las Sierritas, W de Lomas Santiago, 160 m, 10 Jun 1982, *J.C. Sandino 3048* (MO). **Masaya:** Camino entre restaurante Tenampa y Piedra Quemada, 7 Apr 1982, *J.C. Sandino 2540* (MO); P.N. Volcán Masaya, W shore of Laguna de Masaya, 135–145 m, 31 Mar 1980, *W.D. Stevens et al. 16871* (MO), ± 11°59'N, 87°07'W, 135–145 m, 31 Mar 1980, *W.D. Stevens, M. Guzmán & D. Castro 16871* (MO); Laguna de Masaya al NW de la ciudad, 11°58'N, 86°07'W, 100–150 m, 24 Oct 1980, *P. Moreno 4019* (MO); lado NW de la Laguna de Masaya, 12°00'N, 86°08'W,

140 m, 23 Feb 1981, *P. Moreno & A. Lopez 7171* (MO); N de Volcán Santiago, Piedra Quemada, 12°01'N, 86°09'W, [200 m], 5 Aug 1981, *J.C. Sandino 1165* (MO); "Piedra Quemada" lava flow, 1 km NW of Volcán Santiago, [12°01'N, 86°10'W], 350 m, 28 Oct 1976, *D. Neill 1111* (MO); a orillas de la Laguna Masaya, 11°58'N, 86°08'W, 160 m, 21 Jan 1981, *P. Moreno 6140* (MO); Laguna de Apoyo costado Este [probably West, since the department, geographic coordinates, and elevation imply the crater near the west coast], 11°56'N, 86°04'W, ca. 100, 24 Oct 1980, *P. Moreno 3948* (MO).

1i. Diospyros acapulcensis Kunth subsp. **veraecrucis** (Standl.) M.C. Provance, I. García & A.C. Sanders, comb. et stat. nov. (**Figs. 16, 18f–k, 19d**). BASIONYM: *Maba verae-crucis* Standl. Contr. U.S. Natl. Herb. 18:119. 1916. *Diospyros verae-crucis* (Standl.) Standl. Publ. Carnegie Inst. Wash. 461: 80. 1935. TYPE: MEXICO. VERACRUZ: Catemaco, 300 m, 26 Apr 1894, *E.W. Nelson 429* (HOLOTYPE: US-569278; ISOTYPE: US-569277).

Maba purpusii Brandegee, Univ. Calif. Publ. Bot. 7(10): 329. 1920. MEXICO. VERACRUZ: Barranca de Panoaya, [ca. 19°10'N, 96°24'W], Sep 1919, *C.A. Purpus 8516* (HOLOTYPE: UC-204975, internet image!; ISOTYPE: MO, internet image!).

Trees and shrubs 2–25 m tall; **trunk** up to 40 cm in diameter; **stems** glabrous or with some persisting hairs, the young stems puberulent, the hairs sometimes curved, longer wavy subappressed hairs often present towards the shoot apex. **Petioles** minutely winged, (2–)3–6(–6.5) mm long, yellowish-green, glabrate below, puberulent above. **Lamina** membranaceous in spring, becoming chartaceous, (47–)60–105(–120) mm long (shade leaves to 160 mm long), (15–)20–40(–55) mm wide, length to width ratio (2–)2.5–3.5(–4.4) **:** 1, oblanceolate, obrhombic or obovate, sometimes nearly elliptic, *base* acute and short attenuate to cuneate, decurrent on the petiole, *margin* flat, *apex* acutely rounded to acuminate and bluntly pointed, usually mucronulate; **lower lamina surface** sparsely to moderately hairy, the hairs straight, appressed, distally oriented, white to gold, clavate glandular hairs often present, epidermis light olive to brownish-green, sometimes minutely papillose or crystal-papillose, the stomatal apparatus translucent and inconspicuous; **upper lamina surface** sparsely hairy, clavate glandular hairs often present, epidermis darker than the lower lamina surface, papillate or sometimes crystal-papillose. **Venation** arcolanguid to eucamptodromous, yellowish-green to orangish; **midrib** prominent below, hairs straight and appressed, glabrate to hirsutulous or ascending to upright puberulent; **lateral veins** 6–10(–12) per side, finely apparent to prominent below, inconspicuous to finely raised above; **3 veins** usually obscure, sometimes darkened. **Male inflorescences** 1–3-flowered cymes, densely pubescent with minute off-white hairs; **peduncles** 1–3 mm long; **pedicels** 0.5–1 mm long, bracts lanceolate, 1.0–2.5 mm long. **Male flowering calyx** densely hairy outside, the hairs slightly wavy, ascending to subappressed, clavate glandular hairs often present, giving the golden to dark brown epidermis a viscid appearance, *tube* 2–3 mm long, glabrous inside except immediately below the sinuses, *lobes* lance-ovate to ovate, (1–)1.5–3.0(–3.5) mm long, 2–2.5 mm wide; **male corolla tube** 5–7 mm long, 3 mm wide, mostly sericeous outside, the basal 1–2 mm glabrous, or with 3 basal shield-shaped glabrous zones, each 1–2 mm long; **male corolla lobes** lanceolate to ovate, 2–3.8 mm long. **Stamens** 12; **filaments** mostly adnate to the corolla, 0.8–1.5 mm long; **anthers** lanceolate, 2.5–3.0 mm long, often acuminate. **Female inflorescences** solitary, rarely a long-peduncled 3-flowered cyme with aborted lateral flowers. **Female flowering calyx** densely and minutely subappressed curly to wavy-hairy, clavate glandular hairs often present, *tube* subcylindrical, 3–5 mm long, *lobes* broadly rounded, (2.5–)3–5(–6.5) mm long, 4–7(–7.5) mm wide, often with a blunt point; **female corolla tube** cylindrical, thickish, 6–7 mm long, 3–4 mm wide, the upper 2/3–3/4 sericeous outside, lower 1/3–1/4 glabrous, border between the regions ± undulate; **female corolla lobes** ovate to oblong-ovate, sometimes, 3.5–4 mm long, 2 mm wide, the margins somewhat involute; **ovary** flask-shaped to obturbinate and vaguely 3-lobed, 2.5–3 mm long, 2.5–3 mm wide, hairy; **styles** narrow, 2–2.5 mm long, ± fused, spreading distally; **stigmas** bifid; **staminodes** (1–)4–6, resembling fertile stamens, or pale, broad, and inserted on the receptacle. **Fruiting pedicels** stout, (0.5–)1–4.5(–9) mm long, glabrous to moderately hairy. **Fruiting calyx** sparsely hairy outside, the hairs slightly wavy to straight, becoming pale and desiccated, epidermis shiny and viscid, often nearly black, *tube* cupulate, (5–)6–9 mm long, often tearing at the sinuses, usually bulbous at the base, densely hairy inside nearly to the base, the hairs short and thickish to longer and fine, epidermis often with dark blotches, *lobes* obtuse to rounded, (2.5–)3–7(–7.5) mm long, (8–)10–14(–15) mm wide, often abruptly acuminate to a blunt point, reflexed, sometimes just near

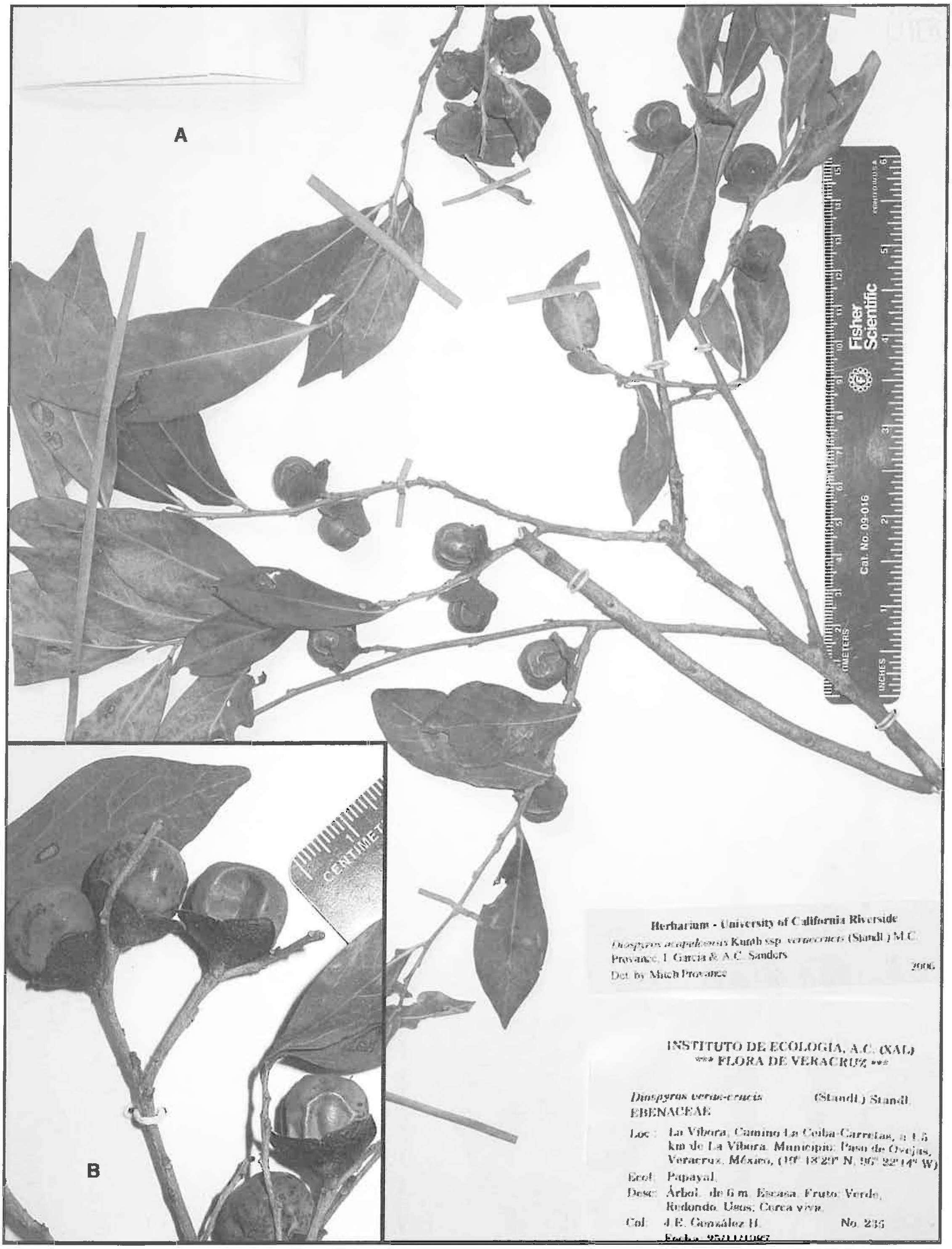

Fig. 16. ***Diospyros acapulcensis*** **subsp.** ***veraecrucis*****. A. Fruiting branchlet from La Víbora, Veracruz (*J.E. González H. 235*, IEB). B. Detail of fruiting branchlet from Cerro de la Mesa, Veracruz (*R. Acosta P. & N. Acosta B. 199*, IEB).**

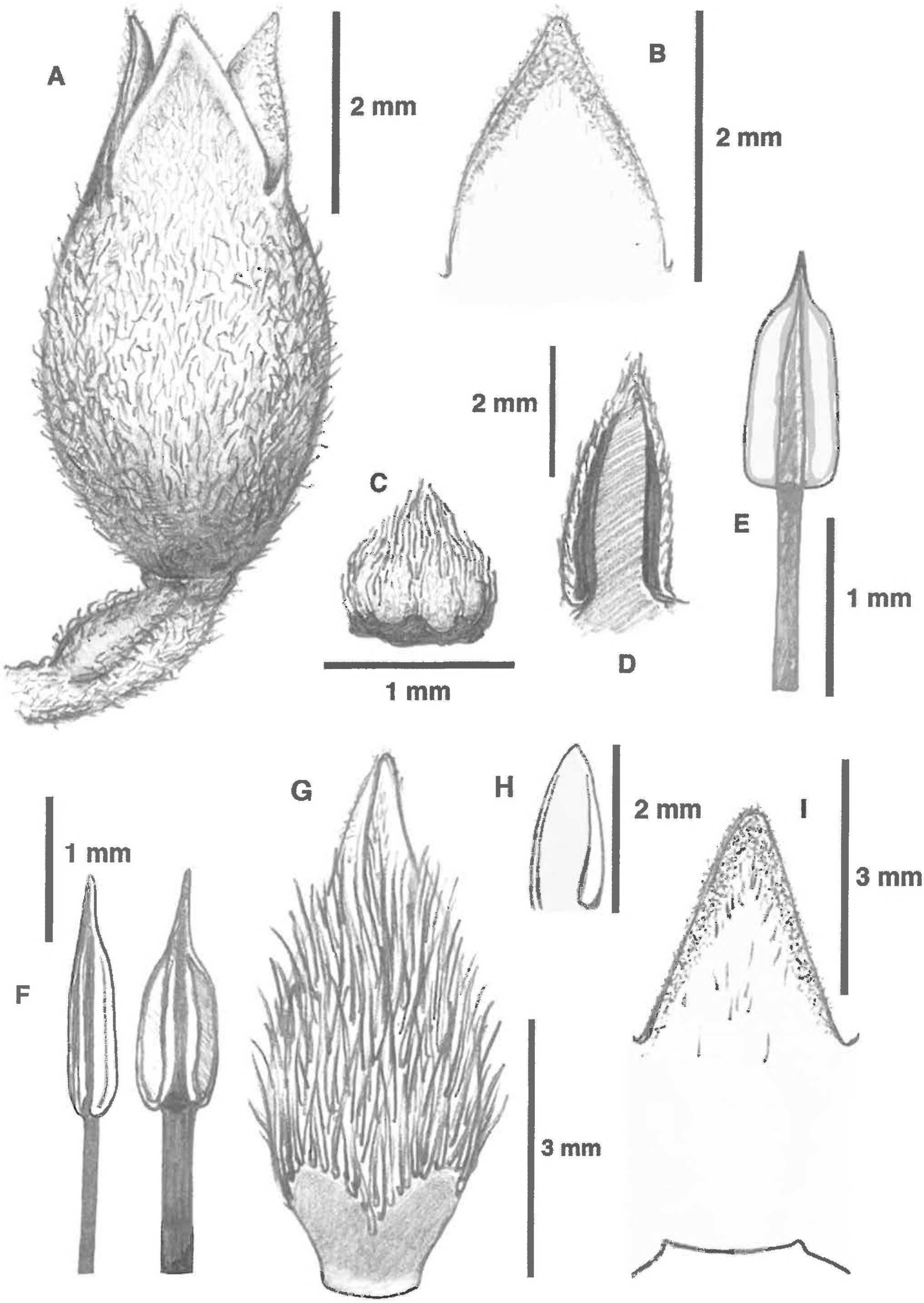

Fig. 17. Flowers of *Diospyros acapulcensis*. A–E. subsp. *rivensis* (pale-leaved form), based on *J.C. Sandino 3048* (MO) from Las Sierritas, Dept. Managua, Nicaragua. A. Immature male flower. B. Adaxial surface of male calyx. C. Pistillode. D. Male corolla lobe (adaxial view). E. Stamen. F–I. subsp. *rivensis*, based on *J.F. Morales 5832* (K) from Punta Agujas, Puntarenas, Costa Rica. F. Stamens (lateral view [left], adaxial view [right]). G. Male corolla. H. Male corolla lobe (adaxial view). I. Adaxial surface of male calyx.

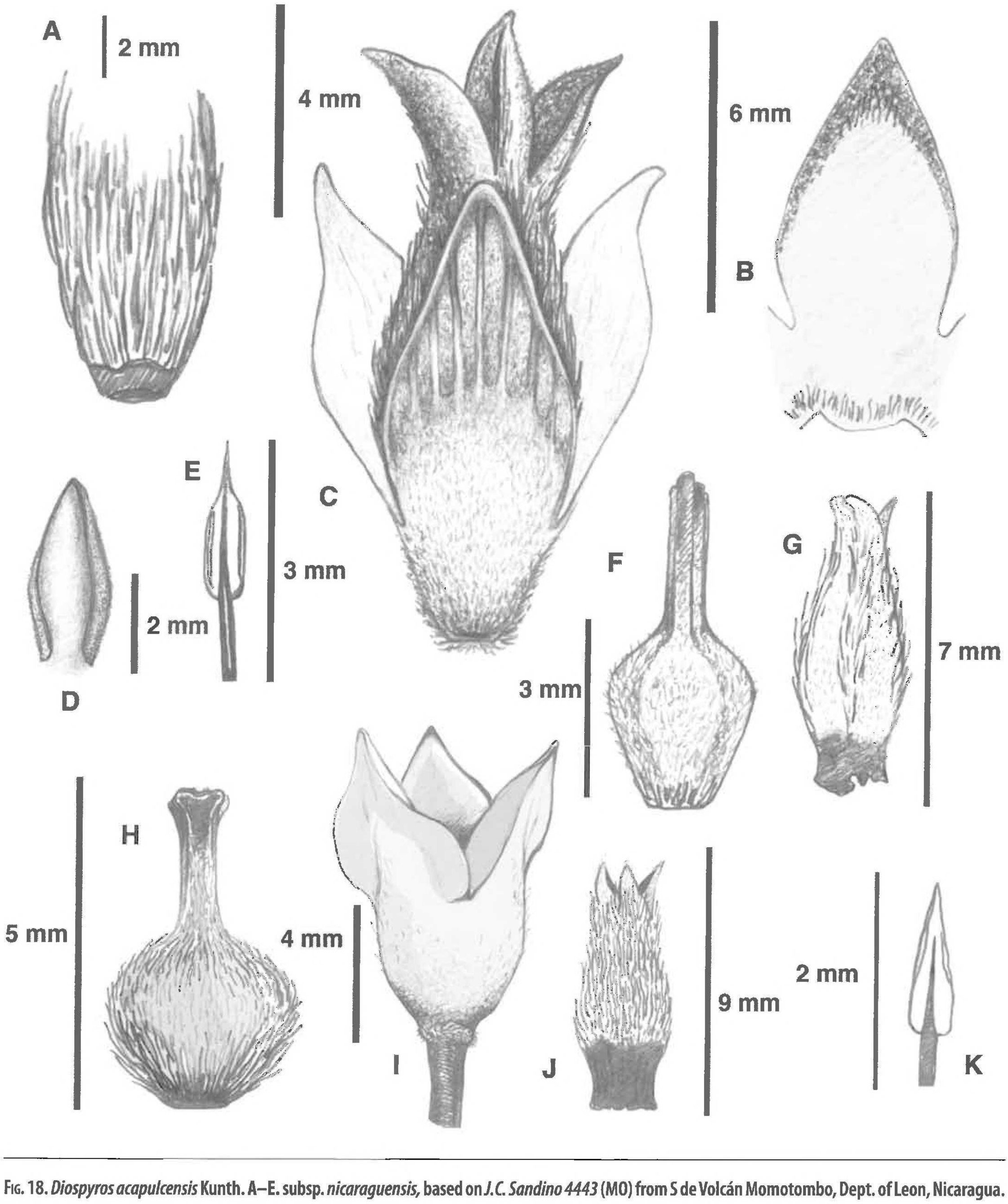

FIG. 18. *Diospyros acapulcensis* Kunth. **A–E.** subsp. *nicaraguensis,* based on *J.C. Sandino 4443* (MO) from S de Volcán Momotombo, Dept. of Leon, Nicaragua. **A.** Adaxial surface of male calyx. **B.** Male corolla tube. **C.** Male flower. **D.** Male corolla lobe (adaxial view). **E.** Stamen. **F–G.** subsp. *veraecrucis,* based on *E. Matuda 5228* (F) from Fraylesca, Chiapas, Mexico. **F.** Pistil. **G.** Female corolla. **H–K.** subsp. *veraecrucis,* based on *B.F. Hansen & M. Nee 7482* from Emiliano Zapata, Veracruz, Mexico. **H.** Pistil. **I.** Female flowering calyx. **J.** Female corolla. **K.** Staminode.

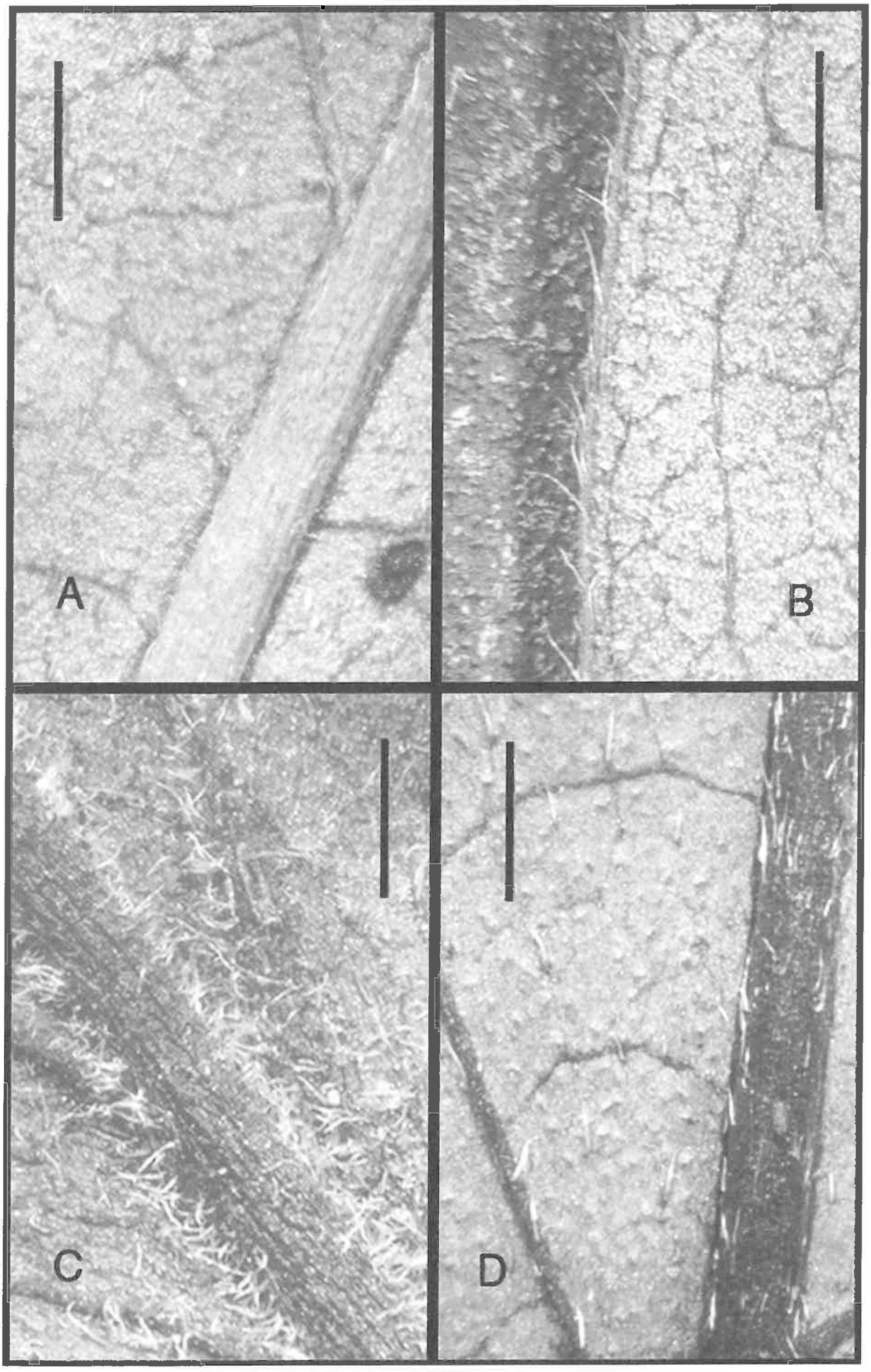

Fig. 19. Abaxial leaf surfaces of *D. acapulcensis* (scale = 1 mm). **A.** subsp. *chiquimulensis,* including midrib and extrafloral nectary (*A. Molina R. & A.R. Molina 12473,* F). **B.** subsp. *chiquimulensis*, margin detail (*A. Molina R. & A.R. Molina 12473,* F). **C.** subsp. *acapulcensis,* including midrib (*J.I. Calzada 9223,* XAL). **D.** subsp. *veraecrucis,* including midrib (*R. Acosta P. 741,* IEB).

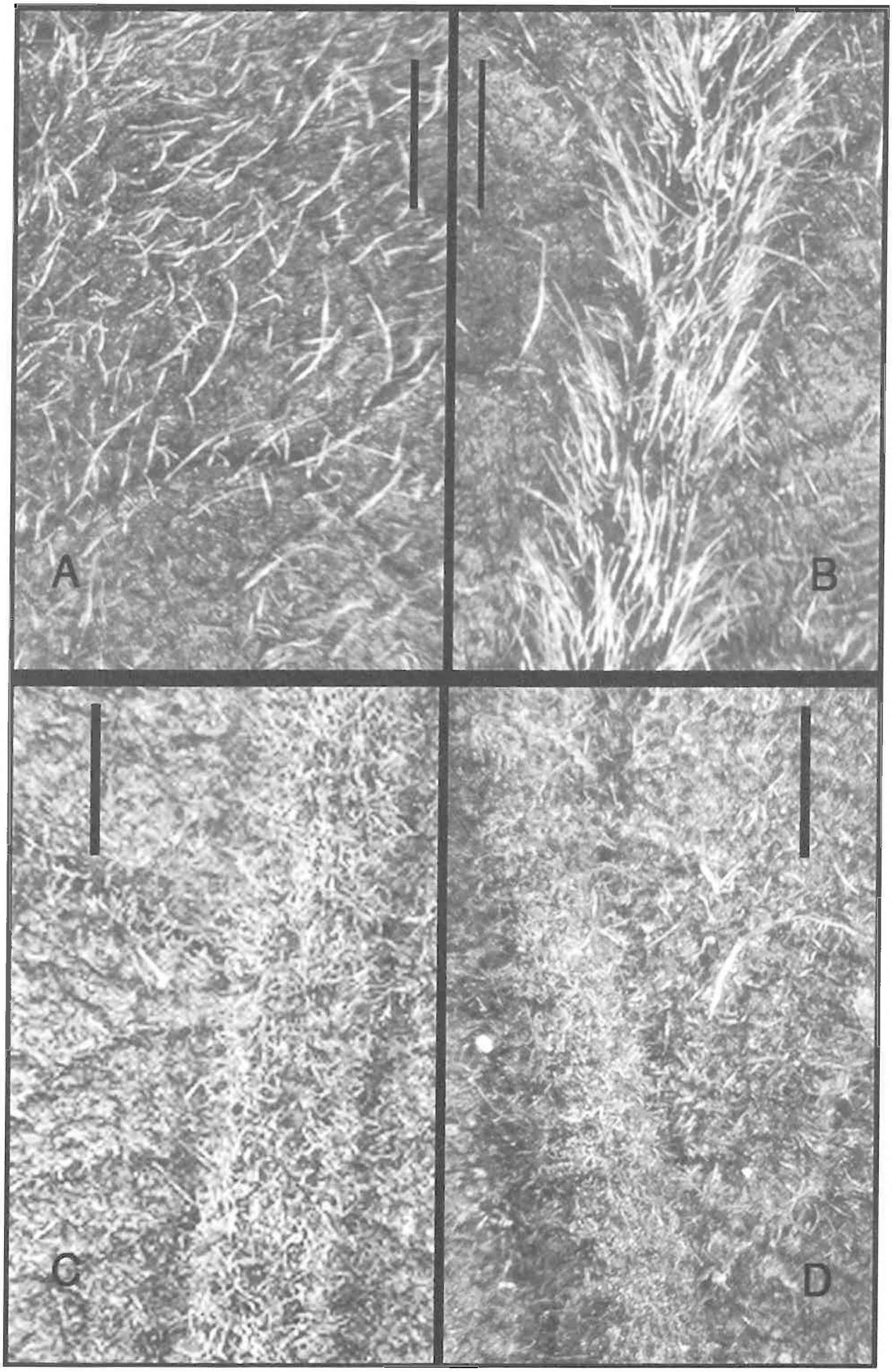

FIG. 20. Abaxial leaf surfaces of *D. acapulcensis* (scale = 1 mm). **A.** subsp. *guanacastensis* (from the holotype). **B.** subsp. *guanacastensis,* including midrib (from the holotype). **C.** subsp. *pedromorenoi,* including midrib (*P. Moreno 10887,* MO). **D.** subsp. *pedromorenoi,* including midrib (from the holotype).

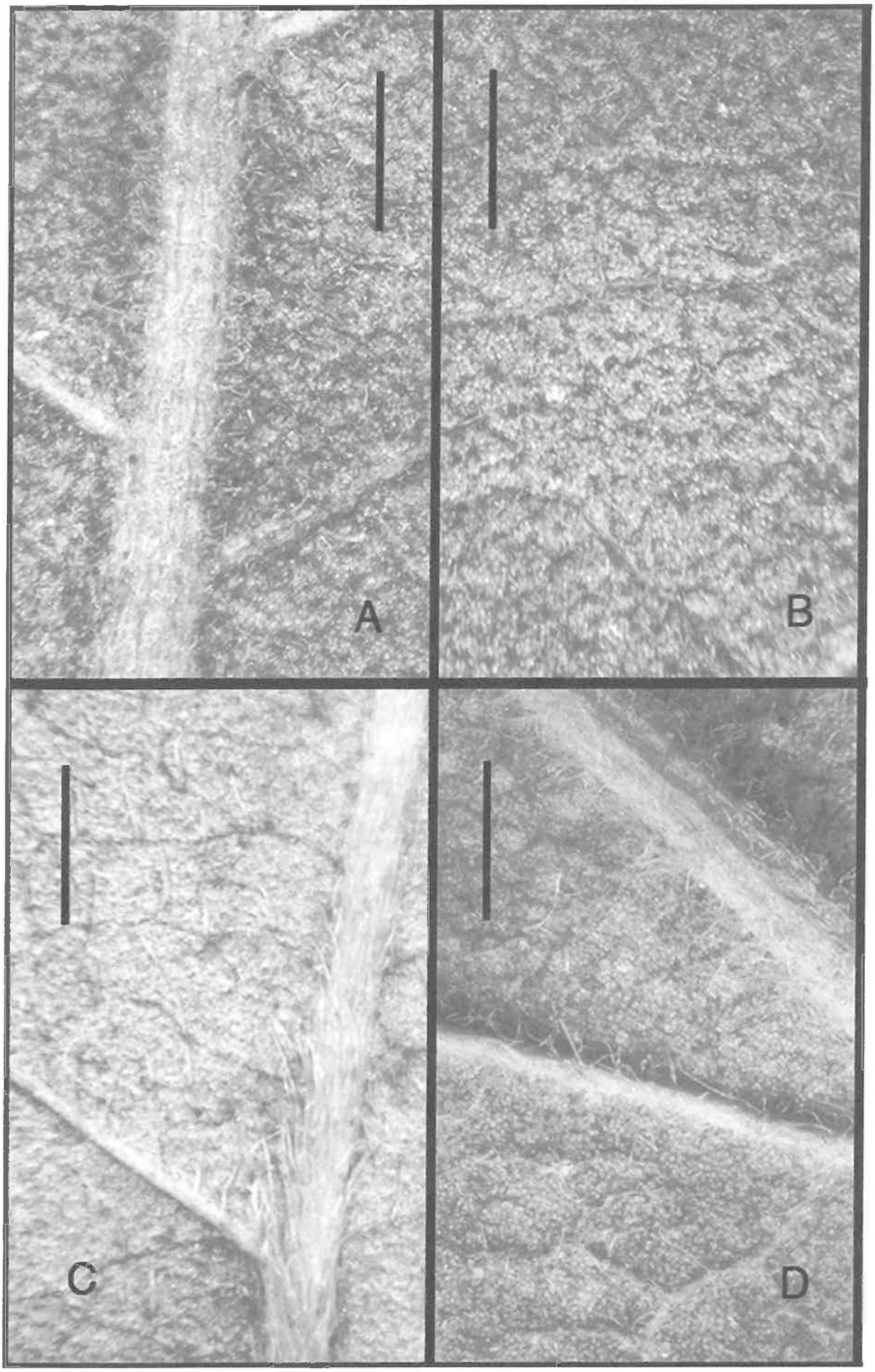

Fig. 21. Abaxial leaf surfaces of *D. acapulcensis* (scale = 1 mm). **A.** subsp. *mejocotensis,* including midrib (from the holotype). **B.** subsp. *mejocotensis,* with detail of epidermis (from the holotype). **C.** subsp. *dwyeri,* including midrib (from the holotype). **D.** subsp. *rivensis* (pale-leaved form), including midrib, from *P. Moreno & J.C. Sandino 6185* (MO).

the apex or along the margins, sericeous inside, the intramarginal band of moderate width. **Fruit** globose, slightly compressed or umbilicate, 2–2.5 cm in diameter, scantily hairy except at apically where densely hairy, epidermis often glaucous-pruinose and scintillant, yellow to light brown, sometimes light reddish-brown, probably golden brown when ripe. **Seeds** 15–16 mm long, 6–7 mm radial depth, 5 mm wide.

This subspecies occurs below 1240 m in tropical deciduous forests, semideciduous forests, and pine forests of El Salvador, Guatemala, Veracruz, Oaxaca, and Chiapas, Mexico (Figs. 23, 24). It has straight, appressed, strictly distally oriented abaxial lamina hairs, versus the straight to wavy, ascending to upright, not strictly distally oriented hairs of *D. a.* subsp. *acapulcensis*. Furthermore, compared to *D. a.* subsp. *acapulcensis*, the leaves of *D. a.* subsp. *veraecrucis* also tend to be slightly longer and narrower relative to length, especially at quarter length. The fruiting inflorescences of some specimens from El Salvador have peduncles 9–13 mm long with aborted lateral flowers that resemble long fruiting pedicels (e.g., *Monro 3576, M.A. Renderos 385*).

There is some suspicion that this taxon should be recognized at the species level, and we considered accepting *Diospyros veraecrucis* Standl. circumscribed so as to include three additional subspecies, all with rather straight, strongly appressed to ascending hairs on the abaxial leaf surface and/or abaxial midrib (e.g., subsp. *chiquimulensis*, subsp. *rivensis*, subsp. *dwyeri*). While we have not seen intermediates between *D. a.* subsp. *veraecrucis* and *D. a.* subsp. *acapulcensis* from regions where their distributions closely approach one another in Chiapas, Mexico, we are also not aware of these taxa occurring together. In the southern part of its range *D. a.* subsp. *veraecrucis* seems to intergrade with *D. a.* subsp. *rivensis* on an island off the coast of southern Honduras. Collections of the complex are lacking from the region between this island and populations of *D. a.* subsp. *veraecrucis* in El Salvador. In turn, *D. a.* subsp. *rivensis* forms intermediates with taxa that have curly or wavy hairs, or hairs not strongly ascending (e.g., *D. a.* subsp. *nicaraguensis*). Consequently, we are following a conservative course in recognizing this taxon only at the subspecific level.

Representative specimens. **GUATEMALA. Esquintla:** Finca Sabana Grande, 550 m, 15 Sep 1997, *M. Nee et al. 47265* (BM); 4 km S of Palín, 7 Aug 1970, *W.E. Harmon & J.D. Dwyer 2945* (UMO). **EL SALVADOR. Ahuachapán:** San Francisco Menéndez, El Corozo, Mariposario, 380 m, 21 Jan 2000, *J.M. Rosales 88* (MO, BM); P.N. El Imposible, 14 Apr 1999, *R. Villacorta & W. Beredsohn 2884* (MO, BM); vicinity of Ahuachapán, 800–1000 m, 9–27 Jan 1922, *P.C. Standley 20328* (MO). **Cabanas:** Cinquera, zona protegida, 380 m, 15 Apr 2002, *R.A. Carballo et al. 206* (MO). **La Libertad:** Canton Guadalupe, 400 m, 27 Nov 1999, *A.K. Monro et al. 3097* (MO, BM); Area protegida San Juán Buenavista, 320 m, 12 Oct 2000, *R.A. Carballo et al. s.n.* (MO); Lavas de Quezaltepeque, 620 m, Dec 1987, *M. Calderón JBL-00582* (MO). **San Salvador:** orilla del Lago de Ilopango, 442 m, 11 Dec 1997, *M.A. Renderos 385* (BM). **Santa Ana:** San José Ingenio, P.N. Montecristo, en el jocotón, 14°25'N, 89°21'W, 1120 m, 24 Sep 2001, *E. Ramos 90* (MO); San José Ingenio, P.N. Montecristo, la vuelta de los pinos, 14°25'N, 89°21'W, 600 m, *V.M. Martínez 240* (MO). Cooperativa Las Lajas, 1240 m, 28 Nov 2000, *A.K. Monro et al. 3576* (MO, BM). **Sonsonate:** Finca Las Victorias, 890 m, 25 Nov 2000, *A.K. Monro et al. 3552* (BM). **MEXICO. Chiapas. Mpio. Acapetahua:** La Encrucijada, 0 m, 26 Jan 1981, *V. Rico-Gray & I. Espejel 329* (XAL). **Mpio. Arriaga:** Río Las Arenas, 15 km NW of Arriaga, 130 m, 27 Aug 1974, *D.E. Breedlove 36833* (MO). **Mpio. Cintalapa:** 3–5 km N of Cintalapa, 900 m, 22 Dec 1972, *E.E. Breedlove & R.F. Thorne 30519* (MO). **Mpio. Mapastepec:** Guadalupe Victoria, 180 m, 22 Nov 1977, *J.I. Calzada et al. 3986* (XAL). **Mpio. Ocozocoautla de Espinosa:** near Derna, 800–1000 m, 16 Dec 1972, *D.E. Breedlove & R.F. Thorne 30360* (MO); 15 km WNW of Ocozocoautla, 800 m, *D.E. Breedlove 28994* (MO). **Mpio. Siltepec:** Fraylesca, 8 Mar 1945, *E. Matuda 5228* (F). **Mpio. Tapachula:** Santa Clara, 100 m, 9 Aug 1984, *E. Ventura & E. López 133* (XAL, MO). **Oaxaca. Mpio. Barrio de la Soledad:** 2 km S de Almoloya, 10 Dec 1980, *R. Cedillo T. & D. Lorence 495* (ILL). **Mpio. Matías Romero:** Campo Nuevo, 28 Apr 1981, *R. Cedillo T. 714* (MO). **Mpio. San Miguel Chimalapa:** 3 km al S de San Miguel Chimalapa, 22 Nov 1983, *R. Torres C. 4132* (MO, CHAPA). **Mpio. San Miguel del Puerto:** 1.6 km al W de Xadani, 500 m, 27 Oct 2001, *A. Saynes V. et al. 2642* (TEX); Finca El Istmo, 790 m, 1 Jan 2001, *A. Saynes V. et al. 2342* (TEX). **Mpio. Santa María Chimalapa:** ca. 6 km en línea recta al NE de Benito Juárez, 1000–1100 m, 3 Sep 1986, *S. Maya J. 3799* (UCR). **Mpio. Santo Domingo Tehuantepec:** "El Mangito," 11.1 km SW de Buenos Aires, 800 m, 25 Nov 1983, *R. Torres C. 4180* (MO). **Veracruz. Mpio. Actopan:** Cerro de la Mesa (Sierra Manuel Diaz), 250 m, 30 Dec 1985, *R. Acosta P. & N. Acosta B. 199* (IEB); Sierra Manuel Diaz, 150 m, 5 Jul 1985, *R. Acosta P. & F. Vazquez B. 741* (XAL, XALU, IEB). **Mpio. Alto Lucero de Gutiérrez Barrios:** Laguna de San Agustin, 10 m, 25 Feb 1983, *C. Gutierrez B. 1304* (IEB). **Mpio. Apazapan:** 2–6 km SE of Emiliano Zapata, 250–400 m, 27 Jun 1980, *B.F. Hansen & M. Nee 7503* (NO, USF, MU, WIS); same location and date, *B.F. Hansen & M. Nee 7482* (FLAS, MO, USF, UMO). **Mpio. Atoyac:** 5 km S de Caballo Blanco, 350 m, 22 Aug 1985, *R. Acevedo R. & F. Vazquez 440* (IEB). **Mpio. Axocuapan:** Ejido Coetzalan, alt 500 m, 6 Nov 1982, *L. Robles H. 358* (IEB). **Mpio. Catemaco:** Isla Agaltepec, lado NW, 24 Apr 1974, *F. Ponce C. & C. Alvarez C. 296* (CHAPA). **Mpio. Comapa:** Barranca de Panoaya, 450 m, 12 Dec 1985, *M.E. Medina A. & M. Ortiz D. 827* (IEB, XAL). **Mpio. Covarrubia:** cerca de Los Mangos, 17 Jan 1972, *R. Hernandez M. 1351* (CHAPA). **Mpio. Dos Ríos:** Plan del Río, 250 m, 25 Jul 1974, *F. Ventura A. 10390* (IEB). **Mpio. Emiliano Zapata:**

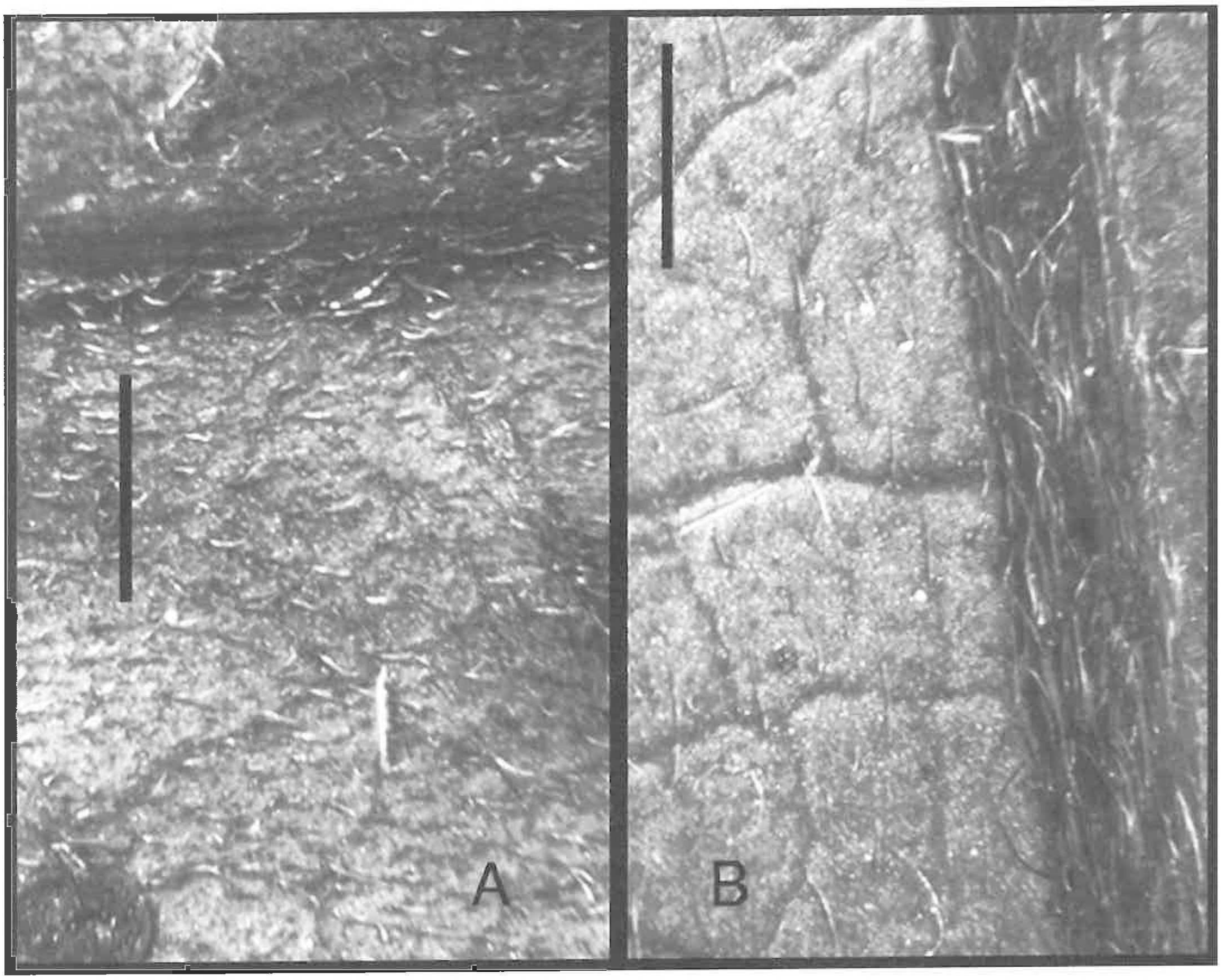

Fig. 22. Abaxial leaf vestiture, including midrib, of *D. acapulcensis* subsp. *rivensis* (scale = 1 mm). A. including nectary (from the holotype). B. *B. Hammel & C. Cano 19581* (K).

Corral Falso, 850 m, 30 Jun 1979, *L. Pacheco & J.I. Calzada 9* (IEB); same location, 17 Jan 1973, *M. Cházaro B. & J. Dorantes 19* (XAL). **Mpio. La Antigua:** Rincón del Pirata, 30 m, 19 Nov 1982, *P. M. Casasola et al. BD-1168* (MO). **Mpio. Medellín:** Paso del Toro, 18 Jan 1990, *P. Zamora C. 1929* (IEB). **Mpio. Naolinco:** cerca de Almolongas, 950 m, 25 Apr 1992, *M. Cházaro B. et al. 6908* (IEB, MO). **Mpio. Paso de Ovejas:** 2 km SW de Cantarranas, 200 m, 30 Jan 1985, *G. Castillo C. & M.E. Medina A. 3551* (XAL, XALU, IEB). **Mpio. Puente Nacional: Chichicastle:** 50 m, 10 Dec 1976, *F. Ventura A. 13729* (IEB). **Mpio. San Andrés Tuxla:** Laguna Encantada, 300 m, 2 Jul 1982, *M. Nee et al. 24761* (BH, USF, WIS). **Mpio. Tamiahua:** E de Laguna Salada, 5 m, 26 Jun 1972, *J. Dorantes et al. 1076* (MO). **Mpio. Tonalá:** NW of Puerto Arista, 3m, 19 Oct 1971, *D.E. Breedlove & R.F. Thorne 20869* (CHAPA, MO). **Mpio. Xalapa:** San Antonio, 800 m, 4 Feb 1975, *F. Ventura A. 10911* (UMO).

2. Diospyros aequoris Standl., Publ. Carnegie Inst. Wash. 461:80. 1935. (**Fig. 25**). *Maba latifolia* Standl. Contr. U.S. Natl. Herb. 18:118. 1916. Type: MEXICO. Sinaloa. [Mpio. Culiacán]: "Collected in the vicinity of Guadalupe" [as on label], "dry coastal thickets" [protologue], [24°15'N, 107°19'W, 3 m], 18 Apr 1910, *J.N. Rose, P.C. Standley & P.G. Russell 14709* (HOLOTYPE: US-637592; ISOTYPES: MO, internet image!, C!). Not *Diospyros latifolia* Gürke, Bot. Jahrb. Syst. 26:63. 1899.

Trees, shrubs, or multi-stemmed clones from root and crown sprouts, 1–8(–12) m tall, facultatively deciduous, dioecious; **trunk** recorded up to 30 cm in diameter, bark nearly smooth (but not slick), irregularly roughened, or irregularly scaly, sometimes fissured or checked, especially at major branch forks, coloration sometimes patchy, usually grayish; **wood** hard, cream to dark yellow, dried branch wood light yellow to golden brown, slash nearly white to light yellow, usually yellowish after several minutes, sap clear; **mature stems** terete, smooth or fissured to half-netted, sometimes somewhat checked, glabrous to scurfy, epidermis often shiny or viscid, variously colored, but mostly beige, reddish-brown, grayish, or castaneous,

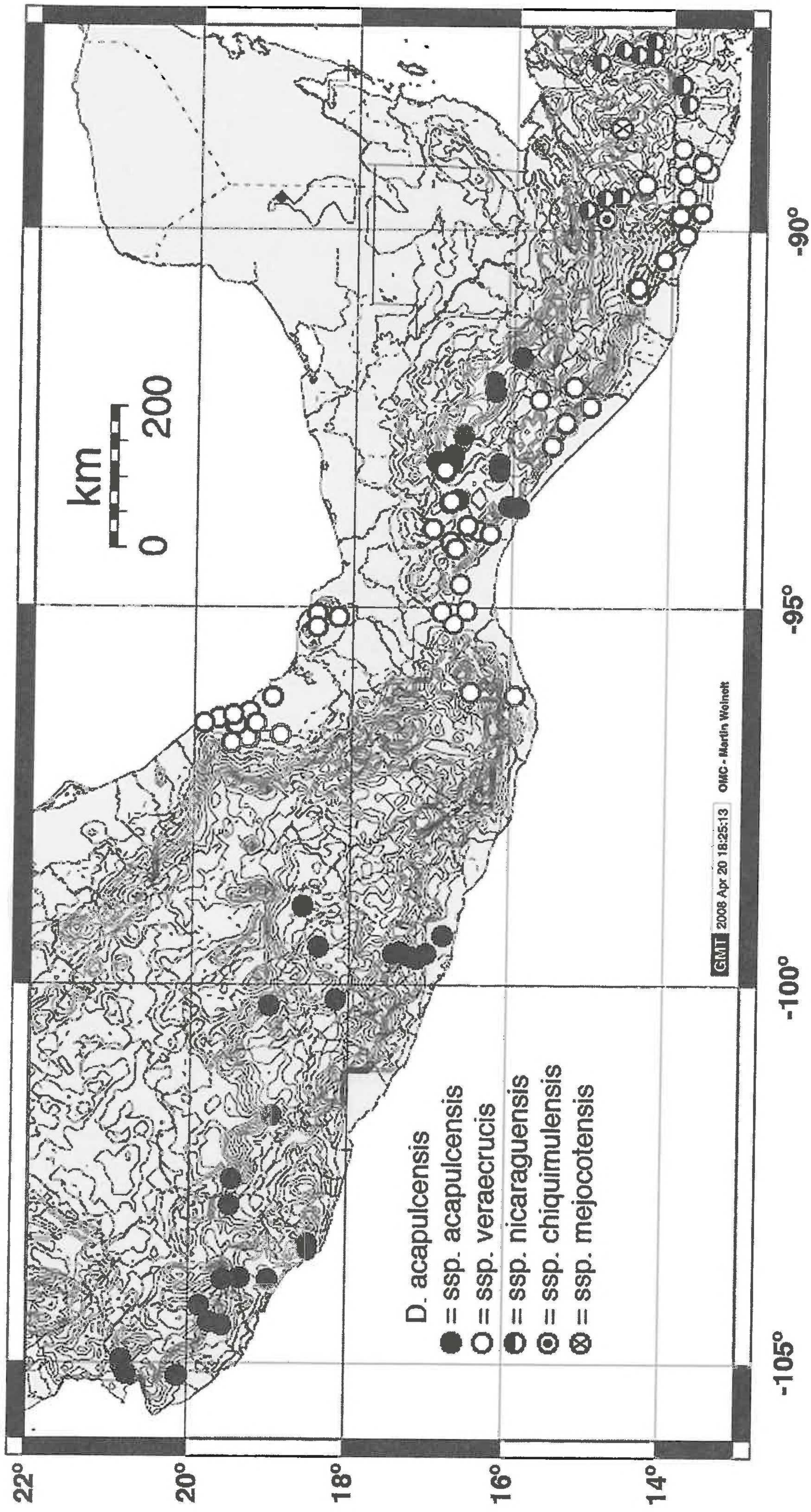

Fig. 23. Distribution of *Diospyros acapulcensis* in Mexico and NW Central America.

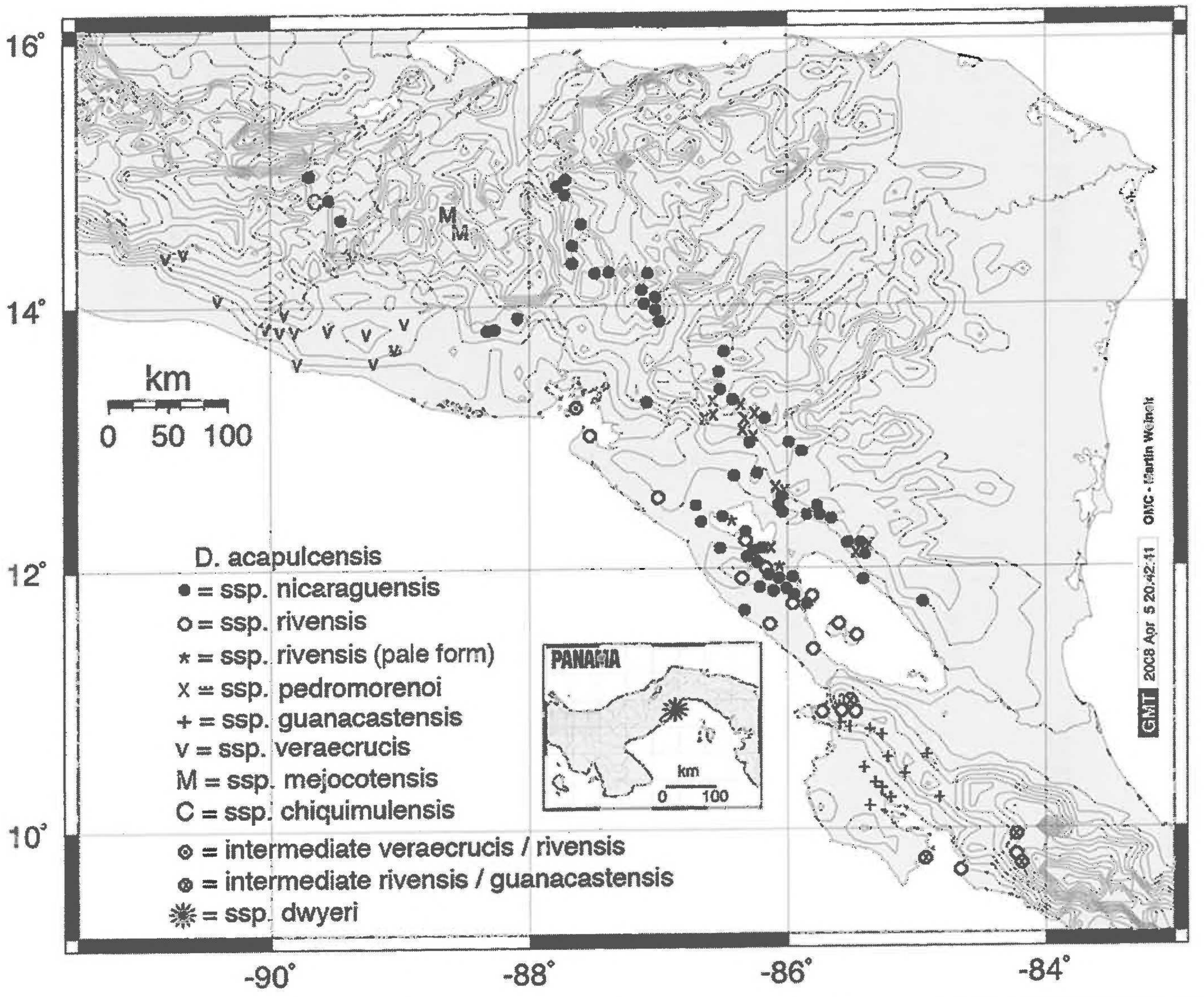

Fig. 24. Distribution of *Diospyros acapulcensis* in Central America.

black gland-dotted, usually lenticellate; **2nd year stems** subterete to terete, sometimes angular, striate to half-netted, often glabrous, or the persisting vestiture desiccated and ashy or covered with exudate, sometimes hispidulous with scattered longer hairs, epidermis coloration variable, minute round cream lenticels commonly present; **1st year stems** angular to terete, smooth or striate to sulcate, densely hairy, the hairs variously straight to curly, minute to about 2 mm long, ascending to spreading, sometimes twisted, clear or white to reddish (the hairs throughout the plant are mostly simple glandular hairs, translucent in life, and the color of hairs in herbarium specimens is due to darkening of a fluid in the lumen), clavate glandular hairs often present, deciduous, leaving the orangish to dark brown (green in life) epidermis viscid. **Leaves** alternate, simple, entire; **petioles** subterete to terete, sometimes broader and flattened or caniculate above, 1.5–6(–7) mm long, margin usually not winged, but sometimes distally so, densely hairy, the hairs as variable as those described for 1st year stems except sometimes subappressed, epidermis smooth to rugose, coloration highly variable, often shiny and viscid; **lamina** chartaceous to subcoriaceous, 18–80(–100) mm long, 12–40(–54) mm wide, length to width ratio 1.1–2.8(–3.2) : 1, usually elliptic, oblong, or oval, *base* mostly rounded to very widely rounded to the petiole (length to width ratio at 1/4 lamina length 1.5–4.3 : 1), clavate glandular hairs often present, but deciduous, the coloration of the epidermis in dry material variable, often darker above than below, *margin* flat to revolute, sometimes undulate, *apex* usually rounded, often widely (leaf length to leaf width at 0.75 length 1.3–3.5 : 1); **lower lamina surface** moderately to densely hairy, the hairs straight, wavy, or curly, minute to 2 mm long, subappressed to upright, white to

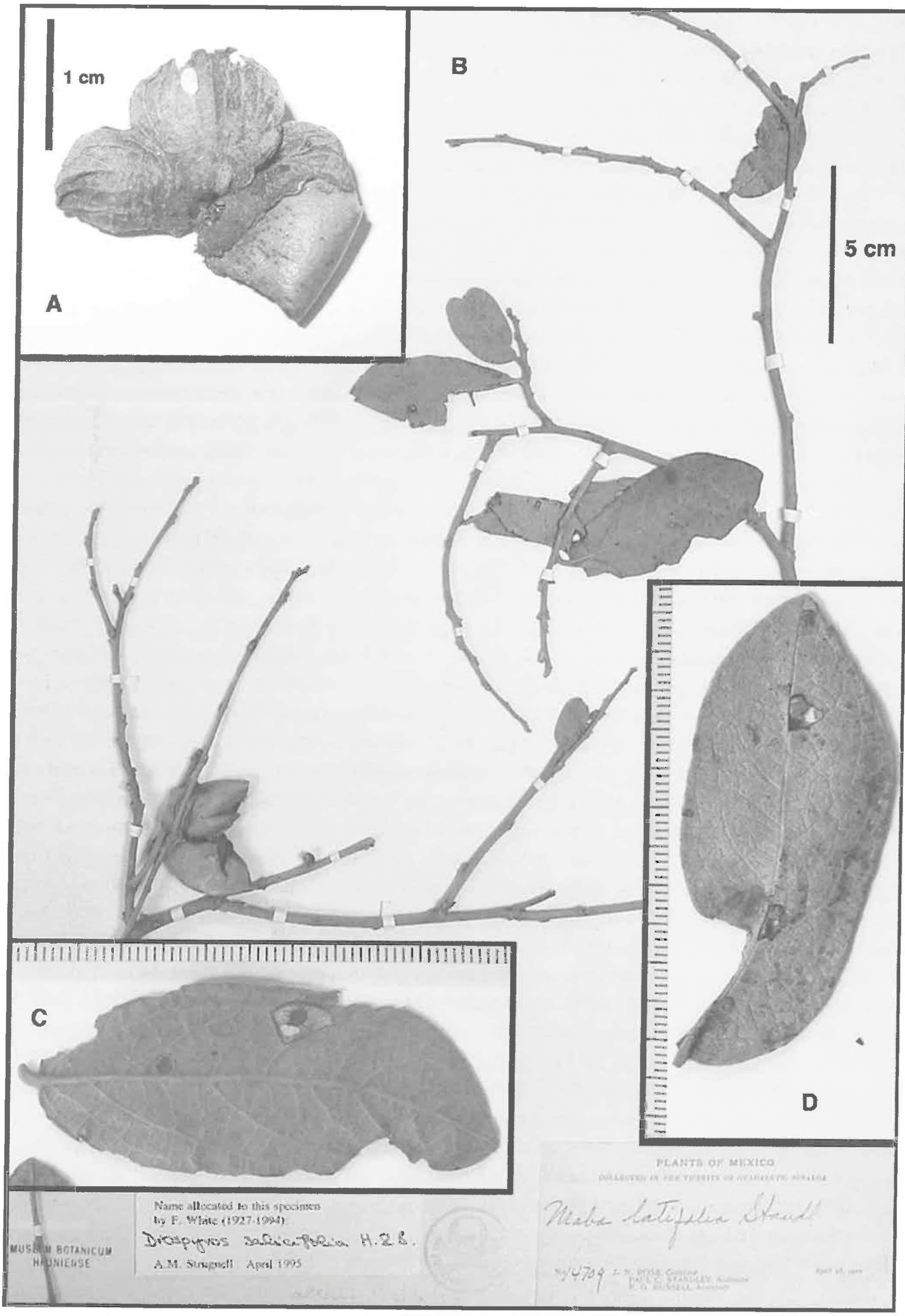

FIG. 25. Isotype of *D. aequoris* Standl. from the vicinity of Guadalupe, Sinaloa (*J.N. Rose et al. 14709,* C). A. Fruiting calyx. B. Leafy and fruiting branchlets. C. Abaxial leaf surface D. Adaxial leaf surface.

dark reddish-brown, vestiture often a mixture of hair types, sometimes deciduous, sometimes persistent and forming patches of desiccated or exudate covered hairs, epidermis dull to shiny or viscid, the stomatal apparatus often opaque, off-white, and conspicuous; **upper lamina surface** usually wrinkled, usually moderately to densely hairy, the hairs as variable as described for the lower lamina surface except usually tending to be erect, often deciduous, the base of the hair sometimes thickened or raised, and forming a seeping annular gland when the rest of the hair falls, the epidermis often shiny and viscid, sometimes crystal-papillose (Fig. 26). **Venation** arcolanguid to brochidodromous, sometimes eucamptodromous, sometimes obscured by the vestiture; **midrib** prominent below, usually densely hairy, but often becoming glabrous, impressed to flush above, sometimes slightly raised near the base, sparsely to densely hairy, the hairs straight to wavy, ascending to upright, clavate glandular hairs sometimes present, sometimes furfuraceous; **lateral veins** (3–)4–9 on each side of the midrib, the course usually tending to arc towards the apex of the leaf with minor inflections, the vestiture and epidermis usually similar to that of the midrib, prominent below, stout to fine, impressed to barely raised above, usually impressed slightly along the lamina-vein seam, sometimes obscure; **3° veins** apparent to prominent below, fine to stout, impressed to obscure above. **Laminar extrafloral nectaries** abaxial, mostly round to oblong, usually 0.3–0.5 mm long, sometimes minutely rimmed, more common in the proximal 1/2 and close to the midrib. **Male inflorescences** solitary 2–3-flowered cymes, or solitary flowers in leaf axils of young stems (usually new growth), densely hairy, the hairs as variable as those described for the lower lamina surface; **peduncles** 0.5–3 mm long; **pedicels** 0.8–5 mm long, bracts deltoid to linear-lanceolate, minute to 2 mm long. **Male flowers** 3–4-merous, ± pendant; **male flowering calyx** narrowly urceolate to narrowly campanulate, sometimes slightly winged, exterior densely hairy, the hairs minute to short, straight to curly, ascending, off-white to golden or tawny, clavate glandular hairs sometimes present, deciduous, leaving the epidermis viscid, light green in life, *tube* 2–4 mm long, 3–4 mm wide, interior usually glabrous, sometimes with scattered to sparse hairs, *lobes* valvate-reduplicate in the bud, acute, 3–6(–7) mm long, 2.5–5(–5.5) mm wide, sometimes with a central keel, exterior densely hairy, interior intramarginal band of hairs variable in width, comprised mostly of minute, curly, off-white to tawny, golden, or reddish hairs, the median glabrous to sparsely hairy, the hairs minute to short, straight to slightly wavy, appressed; **male corolla** white to cream in life; **male corolla tube** salverform to narrowly urceolate or cylindrical, sometimes narrowing distally, 4.5–6.5 mm long, 3–4 mm wide, with three shield-shaped, 0.3–2 mm long, glabrous zones at the base, or sometimes the basal part of the tube completely glabrous, otherwise sericeous with an undercoat of minute curly to straight hairs, minute hairs sometimes present between the sericeous and glabrous zones; **male corolla lobes** spreading in life, lanceolate to ovate, elliptic, oblong, or rhombic, 2–4 mm long, 0.8–2.5 mm wide, densely hairy, the hairs minute, curly to wavy (and then upright), or straight and appressed, especially along the left side, sometimes straight and nearly retrorse or going in random directions, especially along the right margin, the median sometimes raised outside, sericeous, at least basally, margins sometimes involute, especially near the base. **Stamens** 9–12; **filaments** adnate to the tube in 1–2 well-defined tiers or somewhat irregularly, often with some (rarely all) inserted on the receptacle, sometimes geminate, rarely filaments adjoined laterally; **anthers** mostly lanceolate, sometimes oblong, 2–2.7 mm long, sometimes 'eared' (with a minute lobe at the base of the anther on each side of the connective), opening by longitudinal slits. **Pistillode** usually minute, densely hairy, the hairs straight to wavy, lustrous. **Female inflorescences** solitary in leaf axils of young (often 1st year) stems, densely hairy, the hairs and epidermis similar to those seen for male inflorescences; **female flowering pedicels** with hairs and epidermis similar to male inflorescences. **Female flowers** 3–4-merous; **female flowering calyx** mitriform, campanulate to broadly campanulate, exterior densely hairy, the vestiture a variable mixture of short hairs and long hair types, the longer hairs sparse, *tube* usually cupulate, sometimes half-globose, (1.5–)2.3–6 mm long, 3–7 mm wide, *lobes* valvate-reduplicate in the bud, winged, usually broadly rounded to subacute, sometimes acute, 3–8 mm long, 4–8 mm wide, abruptly acuminate or bluntly acute, major nerves sometimes conspicuous; **female corolla** white to cream in life; **female corolla tube** urceolate or short urceolate to subcylindrical, usually narrowing distally, 4–7.5

mm long, (2.5–)3–4 mm wide, exterior vestiture similar to that described for male corolla tubes, interior glabrous; **female corolla lobes** spreading in life, ovate to rhombic, sometimes oblong, (2.5)3–4 mm long, 1.8–2.5 mm wide, often glabrous near the exterior margins, the median often broadly raised outside, often partly involute, exterior vestiture similar to that of male flowers, interior glabrous, sometimes with a longitudinal depression through the center; **ovary** obturbinate, ovoid, globose, ± depressed-globose or somewhat conical, usually about 2 mm in diameter, glabrous to densely hairy, the hairs straight, white, blond, cream, tan tawny, or reddish, sometimes dimorphic; **styles** 3, spreading or fused into a column, 1.8–2.5 mm long, usually with minute appressed hairs on the exterior, interior sometimes with some minute wavy hairs; **stigmas** vaguely bifid to conspicuously v-shaped, rarely trifid; **staminodes** 0–6, adnate to the base of the corolla tube or inserted on the receptacle, narrowly lanceolate, rarely ovate, 2–4.5 mm long. **Fruiting pedicels** terete to angular, sometimes stout, often broader distally, 2–8(–12) mm long, subglabrous to densely hairy, the hairs usually wavy to curly, often covered with exudates, clavate glandular hairs sometimes present, deciduous, leaving the light orange to dark reddish-brown epidermis viscid, bracts 1–2, opposite to subopposite, linear to ovate, 1.5–4 mm long, concave to conduplicate. **Fruiting calyx** slightly accrescent, cupulate to explanate, sometimes tearing at the sinus along a zone of dehiscence, exterior vestiture as described for flowering calyces or glabrate, often with pale desiccated remnants of the original vestiture, epidermis often conspicuously viscid and darkened, *tube* (3–)3.5–6.5(–8.5) mm long, interior glabrous to hairy in the upper 1/2–2/3, the hairs usually straight and appressed, *lobes* obtuse to rounded, overall similar to the calyx lobes of female flowers except wider, rarely acute, 3–8(–9) mm long, (6–)6.5–15 mm wide, reflexed (basally, near the apex, or along the margins), interior intramarginal band of hairs variable in width, the hairs similar to those described for the intramargin of the male calyx, the median usually hairy, the hairs usually straight and appressed. **Fruit** a globose to subglobose or obovoid berry, 1.5–2.5 cm in diameter, consistently with three pairs of locules, glabrous to sparsely hairy, sometimes moderately hairy at the base, often densely hairy at the apex, the hairs slightly wavy to straight, a basal ring of subappressed, fine, straight hairs sometimes present (the ring may adhere to the base of the fruiting calyx tube); **flesh** gelatinous, drying vitreous, reddish and translucent; **epidermis** smooth to orange-peeled or wrinkled, sometimes separating from the fruit wall upon drying, sometimes glaucous, pruinose or scintillant, mature fruit light grayish-yellow to golden brown, green in life, golden brown when ripe. **Seeds** shaped like an orange segment, texture rugulose-foveolate, 11–17 mm long, 6–9 mm radial depth, 5–7 mm wide.

KEY TO THE SUBSPECIES OF *DIOSPYROS AEQUORIS* IN MESOAMERICA

1. Lamina orbicular to oblong or obovate, length : width ≤ 1.6 : 1, base subcordate to rounded, length : width at 0.25 < 2.2 : 1, length : width at 0.75 < 1.7 : 1, margin flat, hairs below fine, soft, glossy, white, sometimes gold; stems atropurpureous; fruiting calyx tube ≥ 5 mm long; mostly trees; Apatzingan Valley, Michoacan, Mexico _____ subsp. **martineziana**
1. Lamina shape variable, but length : width usually > 1.6 : 1, base not subcordate, length : width at 0.25 > 2.2 : 1, length : width at 0.75 > 2.2 : 1, margin often revolute, hairs below not as above; stems light gray to atropurpureous; fruiting calyx tube < 5 mm long; trees or shrubs; Sinaloa to Oaxaca, W Mexico.
   2. Fruit epidermis weakly attached to the fruit wall, often separated in dry specimens, dull light yellow; lamina rhombic, oval, elliptic or oblong, the hairs below cream to yellowish, later ashy; fruiting calyx small (calyx length + lobe width 15–20 mm), the lobes reflexed near the apex; E Michoacan and adjacent regions of Mexico and Guerrero _____ subsp. **balsensis**
   2. Fruit epidermis strongly attached to the fruit wall, usually not separated in dry specimens, not dull light yellow; lamina rarely rhombic, hairs below variously colored; fruiting calyx small to large (calyx length + lobe width 16–28 mm), the lobes reflexed or not; W Mexico.
      3. Lamina chartaceous, not coarsely wrinkled, the margins undulate, not revolute, hairs above deciduous, leaving a seeping glandular area, 2° venation eucamptodromous, 3° venation slightly raised below, inconspicuous above; fruiting pedicels 2.5–4 mm long; coastal W Guerrero, Mexico _____ subsp. **chutlensis**
      3. Lamina subcoriaceous and usually coarsely wrinkled when mature, the margins often revolute, not markedly undulate, hairs above sometimes deciduous, usually not leaving conspicuous seeping areas, 2° venation brochidodromous, 3° venation prominent below, impressed above; fruiting pedicels 2–8(–12) mm long; fruiting calyx small to large; Oaxaca, Jalisco, Nayarit, Sinaloa, Mexico.

4. Fruiting pedicels mostly 5.5–12 mm long; fruiting calyx large, the lobes 11–14 mm wide; lamina usually > 65 mm long, petioles usually > 4 mm long; known only from coastal Oaxaca _____ subsp. **rekoi**

4. Fruiting pedicels mostly 2–5.5 mm long; fruiting calyx small to large, the lobes 6–15 mm wide; lamina usually < 65 mm long, petioles often < 4 mm long; interior Oaxaca, Sinaloa, Nayarit and coastal Jalisco, Mexico.
   5. Lamina bright green to beige or reddish-brown above and below, vestiture below, including the midrib, usually a mixture of curly or kinked hairs with some longer slightly wavy to straight, subappressed hairs, venation below very prominent, greenish to beige, brick red or reddish-brown; plants of Sinaloa, Nayarit and coastal Jalisco, Mexico _____ subsp. **aequoris**
   5. Lamina greenish-gray to gray above and below, vestiture below, including midrib, of wavy to straight hairs, venation below prominent, cream to magenta or speckled with both colors; known only from interior Oaxaca _____ subsp. **tehuantepecensis**

2a. Diospyros aequoris Standl. subsp. **aequoris** (**Figs. 25, 26, 27, 28, 38b**).

Trees or shrubs, 1–4(–9) m tall; **trunk** grayish-white or gray to reddish-brown; **stems** glabrous, furfuraceous, or with remnant patches of desiccated hairs, young stems with short, dense, reddish curly hairs, and sparse long, straight, spreading to ascending hairs. **Petioles** cylindrical to semi-terete, 1.5–4 mm long, densely hairy, the hairs curly, sometimes nearly straight, ascending, reddish-brown, epidermis dark brown, viscid. **Lamina** subcoriaceous, rarely chartaceous, (20–)26–66(–77) mm long, 15–28(–34) mm wide, length to width ratio 1.7–2.7(–3.2) **:** 1, elliptic to obovate, rarely oval, gray to reddish-brown, darker above than below, *base* obtusely rounded, sometimes short-attenuate, *margin* revolute, *apex* obtusely to acutely rounded; **lower lamina surface** with dense reddish-brown tomentum, with some longer slightly wavy to straight, ascending to subappressed hairs, the vestiture deciduous, or becoming ashy and covered with exudate, clavate glandular hairs often present, the epidermis olive-green to brownish, the stomatal apparatus translucent to opaque, usually conspicuous; **upper lamina surface** wrinkled, subglabrous to curly-villosulous, the hairs deciduous, clavate glandular hairs often present. **Venation** brochidodromous, very prominent below, markedly impressed above; **midrib** subsericeous below, with sparse shorter curly hairs, the epidermis viscid, reddish, densely hairy above, the hairs wavy, ascending, furfuraceous, viscid; **lateral veins** 5–7(–8) per side, prominent below, subsericeous; **3° veins** prominent below, wavy-hairy. **Male inflorescences** solitary flowers, with dense minute cream to golden wavy hairs; **pedicel** 4–6 mm long, bracts minute, ± deltoid. **Male flowering calyx** urceolate to subcylindrical, with dense, ascending, cream to golden pubescence, *tube* 2–4.2 mm long, 3–4 mm wide, several straight, 1.5–2 mm long hairs inside near the base, shorter hairs scattered distally, *lobes* narrowly triangular, 3–5 mm long, 2.5–3 mm wide, with scant short vaguely wavy appressed hairs inside, the tomentose intramargin very narrow; **male corolla tube** 5.5 mm long, 3 mm wide, exterior cream to yellowish or reddish sericeous, with 3 shield-shaped glabrous basal regions, each 1.5 mm long; **male corolla lobes** lanceolate to rhombic, 2.5–4.5 mm long, 0.8–2.5 mm wide. **Stamens** 9–12; **filaments** adnate to the corolla in two distinct tiers, or all inserted on the receptacle, 1–1.5 mm long; **anthers** oblong-lanceolate, 2 mm long, sometimes 'eared' basally, vaguely granulate apically. **Female inflorescences** densely and minutely hairy. **Female flowering calyx** campanulate, sometimes broadly, densely reddish tomentulose outside, with some longer spreading hairs, epidermis reddish-brown, viscid, *tube* cupulate, 3–3.5 mm long, 4 mm wide, the upper 1/2 densely hairy inside, lower 1/2 glabrate, *lobes* obtuse, 6–8 mm long, 5–6 (7) mm wide, bluntly pointed to acutely rounded; **female corolla tube** 6 mm long, 2.5–3.3 mm wide, upper half white sericeous outside, lower half glabrous, drying dark red; **female corolla lobes** ovate to oblong, 3.5 mm long, 2.5 mm wide; **ovary** obturbinate to ovoid, minutely white to tan sericeous; **styles** 3, fused most of their length; **stigmas** 3, conspicuously v-shaped; **staminodes** 0–3, inserted on the receptacle, slender, 4.5 mm long, dark red. **Fruiting pedicels** 2–5(–8) mm long, densely tomentulose, clavate glandular hairs often present, epidermis reddish-brown or darker, bracts linear, 1.5 mm long, conduplicate. **Fruiting calyx** rotate to explanate, densely golden to reddish-brown tomentulose outside, with occasional longer straight hairs, glabrate, or the hairs desiccating, becoming ashy, and sticking to the viscid epidermis,

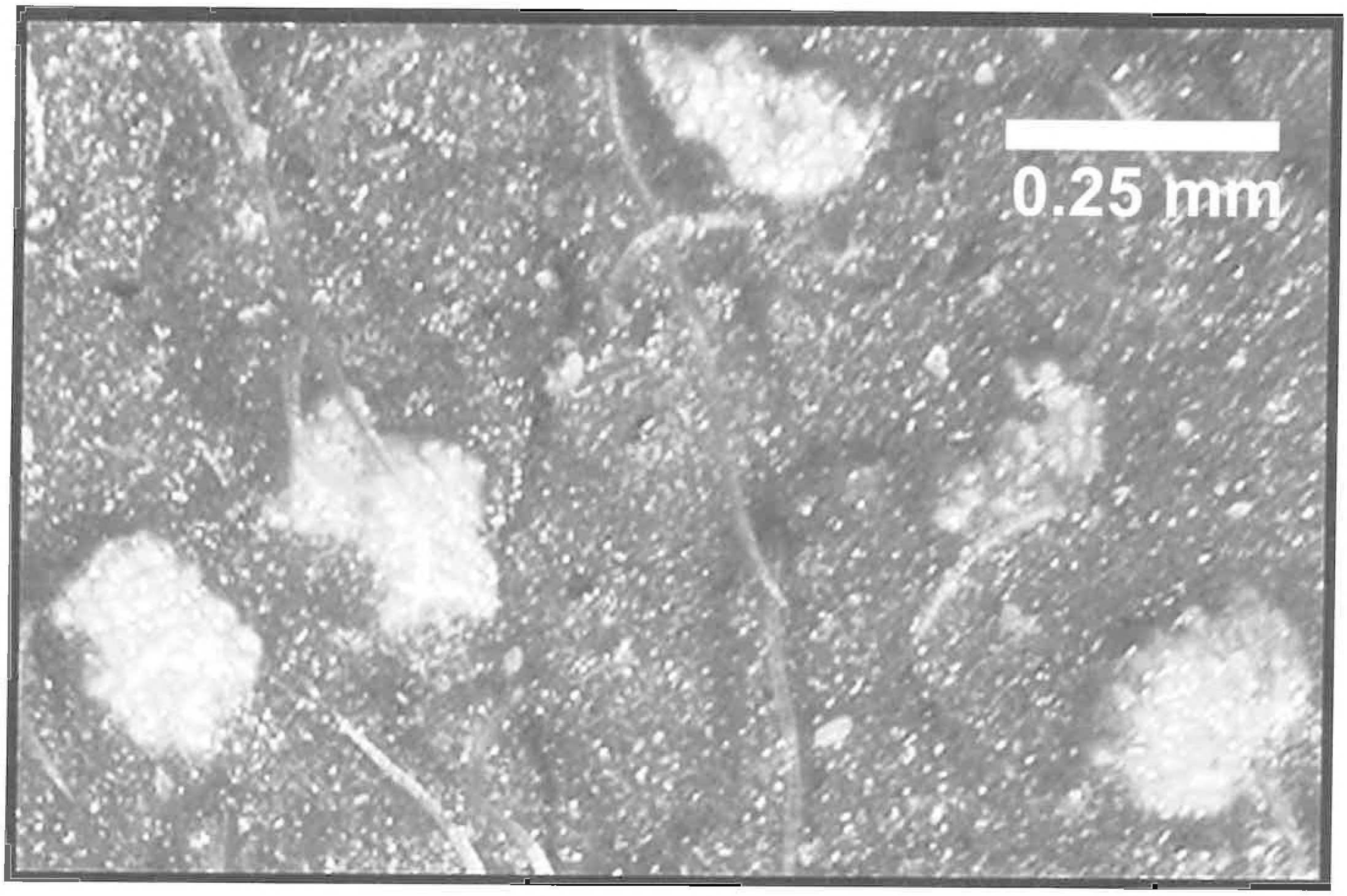

Fig. 26. Detail of adaxial lamina epidermis with aggregates of albescent excrescences (crystal-papillose) in *D. aequoris* subsp. *aequoris* (*Provance 9593*, UCR).

tube (3–)4–6.5(–9) mm long, the upper 1/2–2/3 hairy inside, lower 1/2–1/3 glabrous, *lobes* acute to slightly obtuse, (4–)5–7.5(–9) mm long, (6–)8–13(–15) mm wide, spreading, or sometimes reflexed near the apex, along the margins, or both, nerves often conspicuous, hairy inside, the interior intramarginal band wide. **Fruit** globose, 1.5–2.5 cm in diameter, densely ascending wavy-hairy basally and apically, glaucous-pruinose and scintillant, yellow to dark golden brown, sometimes black gland-dotted. **Seeds** 12–13 mm long, 6–7 mm radial depth, 5 mm wide.

This subspecies occurs in semi-arid oak forests on rocky soils in the Barranca Region of the west Durango-Sinaloa border region, on steep, rocky volcanic slopes with dry tropical forest in the foothills around Culiacan, on the coastal plains of Sinaloa in thornscrub and dry tropical forest or thornscrub transitioning to mangrove forest, and on inland mesas with *Krameria* in the northern extremity of Nayarit. Several, apparently disjunct, populations occur on and near the coast of Jalisco in the vicinity of the Bahia de Chamela (Fig. 40). Only two specimens with male flowers have been seen. In both cases the inflorescences consisted of solitary flowers in leaf axils of new growth, representing exceptions to the 3-flowered cymes typically seen in the complex. This subspecies is similar to *D. ae.* subsp. *tehuantepecensis* from inland Oaxaca, being separated by differences (see key) in leaf surface, abaxial leaf vestiture, and lamina color (at least when dry). Furthermore, ratio of leaf length to average distance between centermost lateral veins is significantly higher in *D. ae.* subsp. *aequoris* than *D. ae.* subsp. *tehuantepecensis*.

Representative specimens: **MÉXICO. Durango. Mpio. Tamazula de Victoria:** Sierra Tres Picos, [25°3'N, 107°1], 3000 ft,19 Dec 1939, *H.S. Gentry 5286* (NA, MO). **Jalisco. Mpio. La Huerta:** Rancho Cuixmala, 200–300 m, 5 Nov 1991, *E.J. Lott et al. 4159* (UCR). **Nayarit. Mpio. Huajicori:** Zonteco, 110 m, 30 Aug 2004, *M.C. Provance et al. 9606, 9607 & 9608* (UCR). **Sinaloa. Mpio. Badiraguato:** Cienegita, SE of Badiraguato, 2000 ft, 29 Mar 1940, *H.S. Gentry 5946* (NA, MO, ARIZ). **Mpio. Cosalá Vado Hondo:** a 14 km del poblado de Cosalá, 590 m, 9 Nov 1985, *A. García V. 172* (CHAPA). **Mpio. Culiacán:** ± 4 km al sur de Culiacán, 50 m, 1 Nov 1990, *R. Vega A et al.*

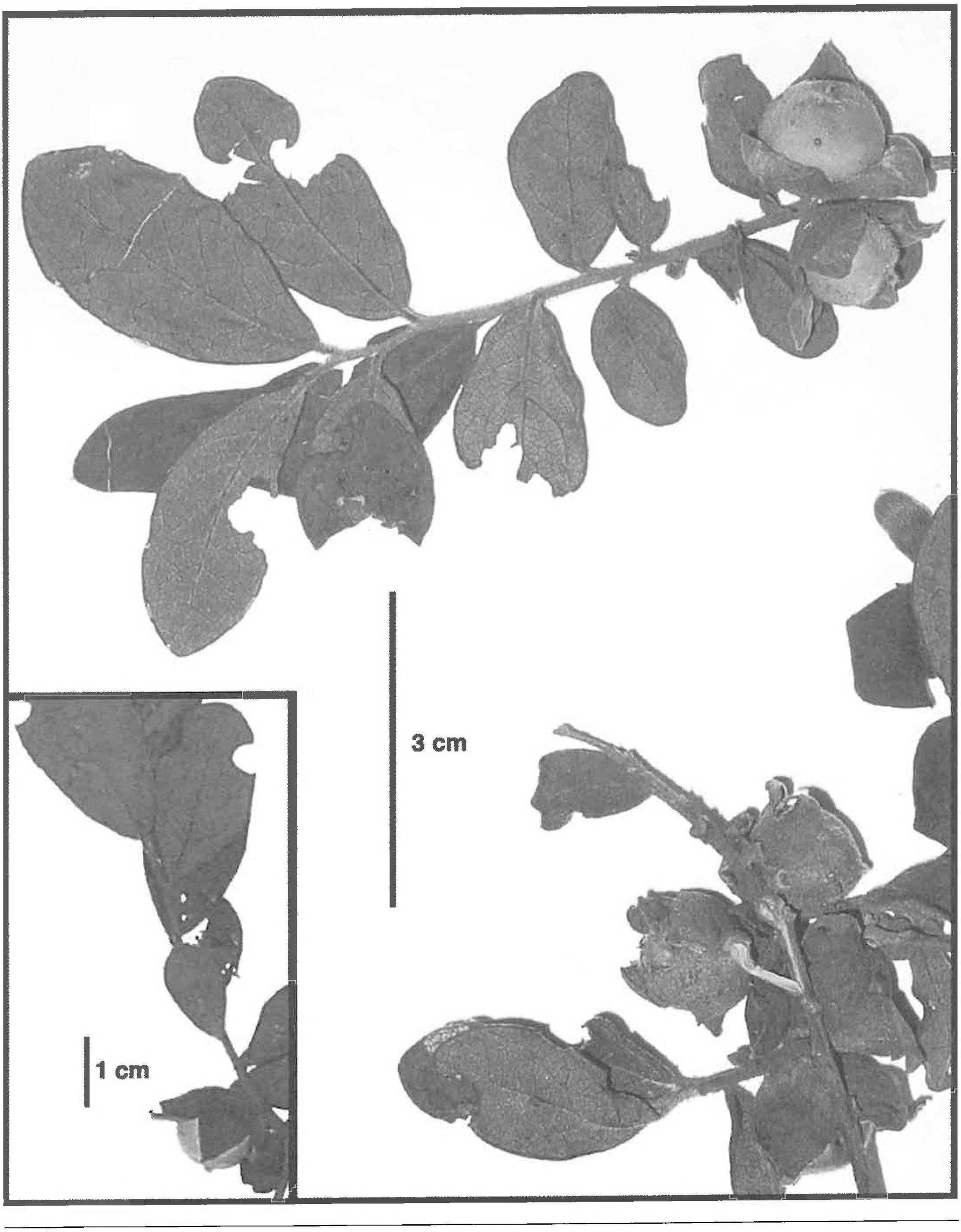

Fig. 27. *Diospyros aequoris* subsp. *aequoris* from 2 km SSW of Vigas Loma, Sinaloa (*M.C. Provance & J.S. Ross-Ibarra 9525*, UCR).

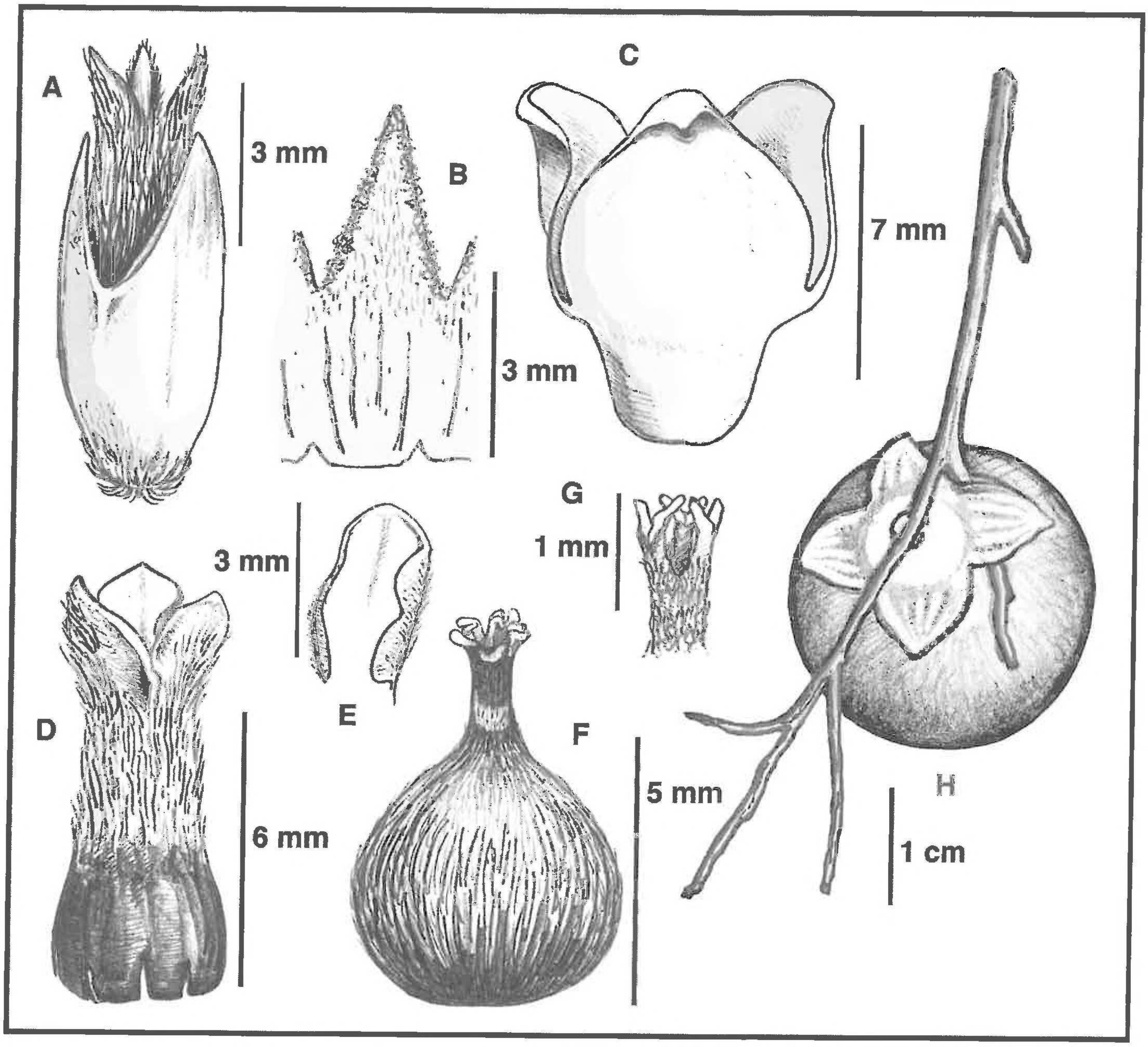

Fig. 28. *Diospyros aequoris* subsp. *aequoris*. A–B. Male flower, based on *Provance et al* 9593, UCR. C–G. Based on *E. Guízar N. 3233* (CHAPA). C. Fruiting calyx. D. Female corolla. E. Female corolla lobe (adaxial side). F. Immature fruit. G. Detail of styles and stigmas. H. Mature fruit, based on *H.S Gentry 5946*, ASU.

3972 (CIIDIR). **Mpio. El Rosario:** Playa de Chametla, ± 9 km S de Chametla, 10 m, 5 Nov 2004, *J.M. Aguilar P. 1608* (UCR); El Carrizo, ± 9 km al N de Cacalotán, 50 m, 6 Nov 2004, *J.M. Aguilar P. 1612* (UCR). **Mpio. Mazatlan:** Isla de la Piedra, 23 Jul 1994, *E. Guízar N. 3233* (CHAPA, IEB). **Mpio. Mocorito:** El Alamo, along road from Mocorito to Surutato, 1500 ft, 3 Mar 1971, *D.E. Breedlove 19111* (MO). **Mpio. San Ignacio:** ca. 2 km SSW of Vigas (Loma) and ca. 10 km WNW of Duranguito, 14 m, 26 Aug 2004, *M.C. Provance & J.S. Ross-Ibarra 9525* (UCR).

2b. Diospyros aequoris Standl. subsp. **balsensis** M.C. Provance, I. García & A.C. Sanders, subsp. nov. (**Figs. 29, 30, 37j–m, 38c**). Type: MEXICO. Michoacan. Mpio. Tuzantla: km 68 carr. B. Juarez–Tuzantla, [19°14'N, 100°30'30"], 790 m, bosque tropical caducifolio, 16 Dec 2004. *I. Garcia R., M.C. Provance & J.A. Machuca 6863* (holotype: CIMI!; isotype: UCR!, and to be distributed).

Frutices vel arbores a *Diospyros aequori* ssp. *aequori* similis sed differt laminis foliorum plerumque latioribus, praesertim ad 1/4 et 3/4 longitudinem, lobis calycis fructiferi brevioribus, et fructibus epidermide infirme affixa.

Shrubs, sometimes arborescent, 1.5–3(–5) m tall; **trunk** smooth to somewhat roughened, bark forming large patches, varying from light to dark gray; **stems** glabrous when mature, but the young stems moderately

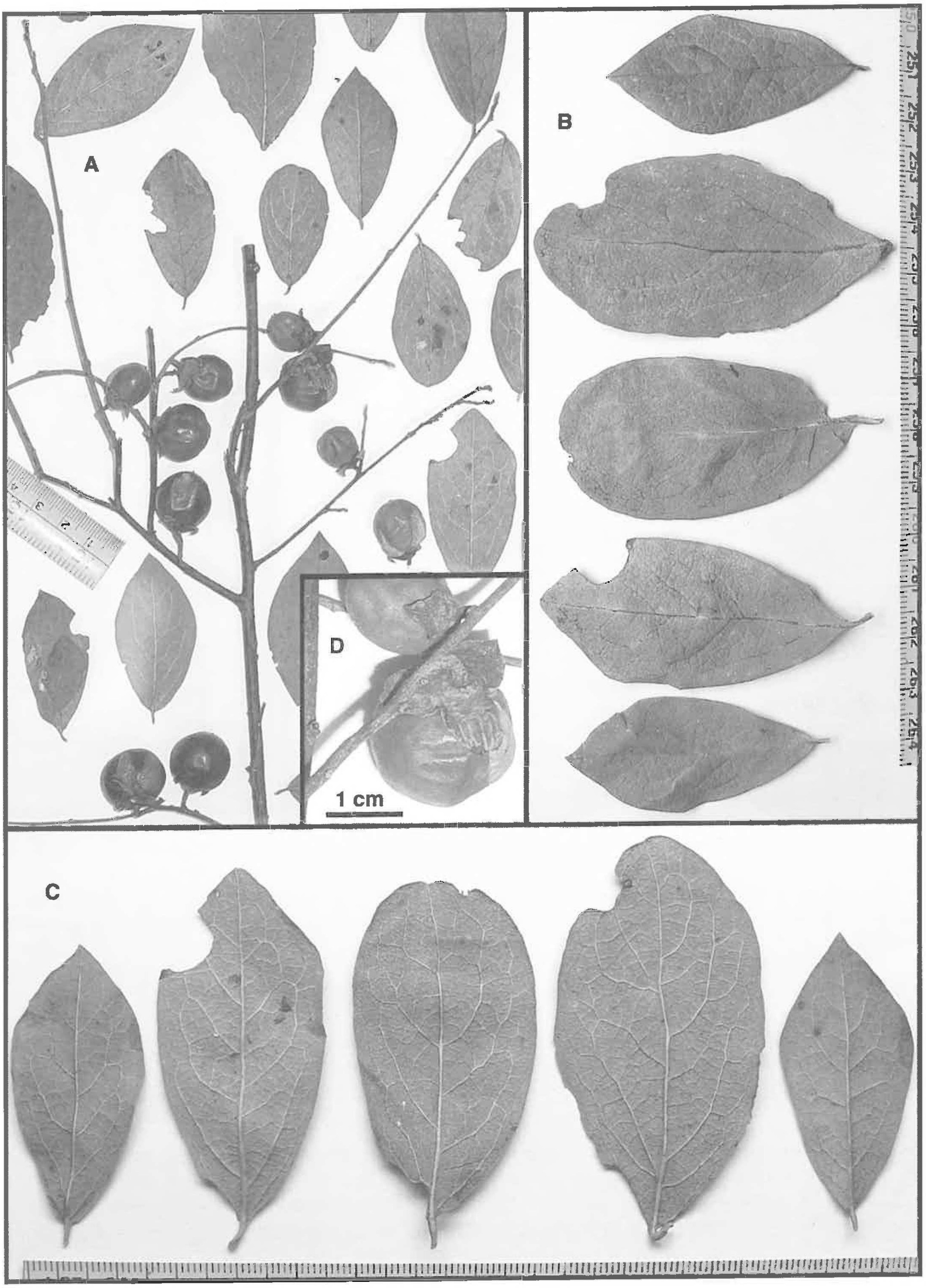

FIG. 29. The holotype of *D. aequoris* Standl. subsp. *balsensis* M.C. Provance, I. García & A.C. Sanders, subsp. nov. from km 68 carr. Benito Juarez–Tuzantla (*I. Garcia R. et al. 6863,* CIMI). **A.** Fruiting branchlet. **B.** Leaves (adaxial surface). **C.** Leaves (abaxial surface). **D.** Fruit detail.

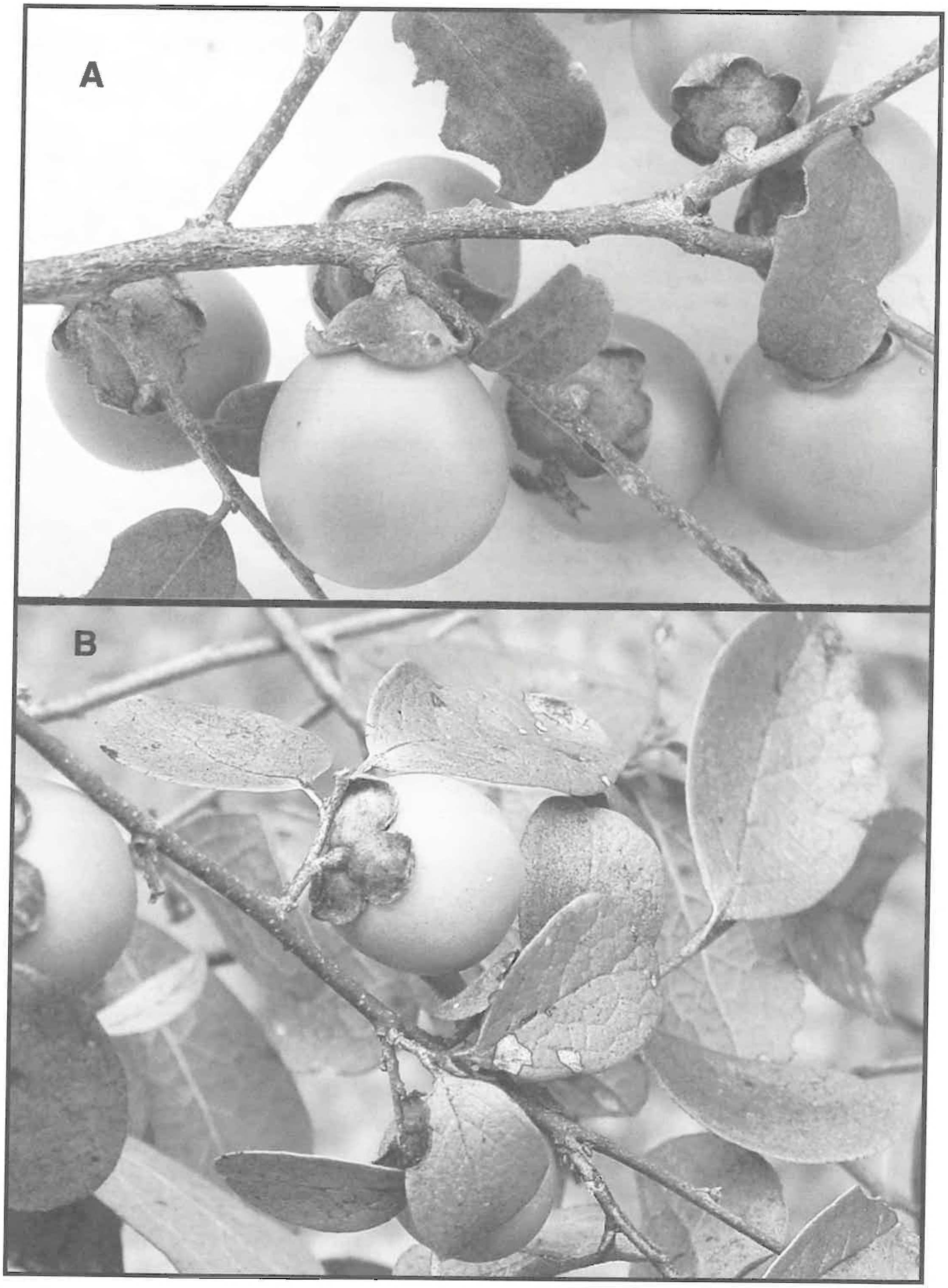

FIG. 30. *Diospyros aequoris* subsp. *balsensis* from km 68 carr. Benito Juarez–Tuzantla. A. Side view of the calyx and obovoid fruit. B. A fruit with slightly torn sinuses and subcoriaceous leaves with markedly impressed venation on the adaxial surface.

ascending hairy, the hairs wavy, sometimes twisting, clavate glandular hairs also present. **Petioles** 2–3(–5) mm long, cream to yellowish tomentulose, with sparse longer slightly wavy hairs, older leaves sometimes glabrate, the epidermis viscid, densely hairy above, the hairs straight to wavy, ascending to upright, cream to yellowish. **Lamina** subcoriaceous when mature, (30–)36–60(–72) mm long, 23–36(40) mm wide, the length to width ratio 1.5–2(–2.6) : 1, rhombic, elliptic or oval, *base* rounded, sometimes attenuate, *margin* slightly revolute, *apex* acutely to broadly rounded; **lower lamina surface** densely cream to yellow villous-velutinous, the hairs sometimes subappressed near the apex, becoming desiccated, pale and ashy, or covered with droplets of exudate, clavate glandular hairs often present, the stomatal apparatus opaque, white, and conspicuous; **upper lamina surface** wrinkled, the vestiture similar to but less dense than on the lower lamina surface, epidermis shiny, pale light green or gray to dark gray in herbarium material, sometimes crystal-papillose. **Venation** brochidodromous, the epidermis yellowish, prominent below, villous-velutinous, sparser above; **midrib** flush to slightly impressed above, impressed along the midrib-lamina seam; **lateral veins** (5–)7–9 per side, impressed above, or flush and impressed along the lamina-midrib seam; **3° veins** prominent below, impressed above; **4°–5° veins** slightly impressed above. **Male inflorescences** 2–3-flowered cymes; **peduncles** ± 2 mm long; **pedicels** 0.8–2 mm long, densely wavy-hairy, bracts linear-lanceolate, ± 1-2 mm long, conduplicate. **Male flowering calyx** narrowly campanulate to urceolate-campanulate, thinnish, cream, tawny or golden tomentulose outside, clavate glandular hairs often present, the epidermis golden brown, viscid, *tube* 2.8–3.2 mm long, glabrous inside, *lobes* acutely triangular, 3–3.3 mm long, 2.8–3.2 mm wide, glabrate inside, except for some scattered retrorse hairs and a narrow intramarginal band; **male corolla tube** 5.5–6.5 mm long, 3 mm wide, golden sericeous outside, with 3 shield-shaped glabrous basal regions, ± 2 mm long, bordered distally by minute wavy hairs; **male corolla lobes** obovate to rhombic, 2.0–2.5 mm long, 1.5 mm wide, margins sometimes involute. **Stamens** 12; **filaments** in two subgeminate tiers adnate to the corolla near the base, up to 2 mm long, reddish- brown; **anthers** lanceolate to narrowly lanceolate, up to 2.7 mm long. **Female inflorescences** densely pinkish-orange tomentulose. **Female flowering calyx** campanulate, narrowly winged, *tube* cupulate, 2–4 mm long, 3 mm wide, the basal 1/2–1/3 glabrous inside, upper 1/2–2/3 sericeous, the intramarginal band wide, pinkish-orange short wavy-hairy outside, with sparse straight ascending hairs, *lobes* thickish, acute, 5–5.5 mm long, 4–4.5 mm wide, vaguely acuminate to a blunt point; **female corolla tube** 6 mm long, 3.5 mm wide, pinkish-orange sericeous outside, with 3 small glabrous shield-shaped basal regions; **female corolla lobes** ovate, 2.5–3.5 mm long, 1.8–1.9 mm wide; **ovary** ovoid, 2.5 mm long, 2 mm wide, hirsutulous to stiffly ascending hairy, the hairs light blond; **styles** 3, fused basally, spreading; **stigmas** bifid to trifid, long, spreading; **staminodes** 5, narrowly lanceolate, up to 4.5 mm long, adnate to the base of the corolla, rarely inserted on the receptacle. **Fruiting pedicels** stout, 2–4(–6) mm long, sparsely to densely wavy-hairy, bracts 1–2, linear-lanceolate to ovate, 3–4 mm long, ± conduplicate. **Fruiting calyx** shallowly rotate to explanate, *tube* 4–6 mm long, hairy, *lobes* widely rounded, (3–)4–5.5 mm long, (8–)9–11 mm wide, apex sometimes cuspidate, reflexed. **Fruit** globose to obovoid, 1.5–2.5 cm in diameter, glabrous to sparsely ascending puberulent, epidermis tending to separate from the remainder of the fruit upon drying, dull yellow to golden brown, in living material greenish-yellow to yellow when mature, golden brown when fully ripe. **Seeds** 16–17 mm long, 9 mm radial depth, 5–7 mm wide.

This subspecies grows in dry tropical forest on slopes and mesas between 600 and 800 m in the Sierra Madre Occidental near the west end of the Sierra Madre del Sur in eastern Michoacan, western Guerrero, and the southwest part of the State of Mexico (Fig. 39). In this subspecies the epidermis of the fruit is weakly attached, a character useful in separating it from similar taxa. It is distinguished from *D. ae.* subsp. *martineziana* by thicker, wrinkled, frequently revolute lamina with a different shape. Lamina shape ratios (i.e., length : width, length : width at 1/4 length, length : width at 3/4 length) being significantly higher in *D. ae.* subsp. *balsensis*. In addition to differences in abaxial vestiture, the lamina of *D. ae.* subsp. *chutlensis* is thinner, less wrinkled, and has an undulate margin. The venation in *D. ae.* subsp. *balsensis* is more prominent than in *D. ae.* subsp. *chutlensis*. This subspecies is similar to *D. ae.* subsp. *aequoris*, but has shorter fruiting calyx lobes, and the lamina is usually wider.

Specimens examined: **MÉXICO. Guerrero. Mpio. Ajuchitlán del Progreso:** Cuahuilote, 29 Jan 1934, *G.B. Hinton et al. 5568* (DES, K). **Mpio. Coyuca de Catalán:** Paso de Arena, 5 Jun 1934, *G.B. Hinton et al.* 6117 (NA, K). **Mpio. Zirándaro de los Chávez:** A 14 km al SW del Tálamo, 710 m, 6 Sep 1982, *J.C. Soto N. & G. Silva R. 4364* (XAL). **México. Mpio. Temascaltepec:** Bejucos, 610 m, 22 May 1933, *G.B. Hinton 3959* (K); same location, 28 Nov 1934, *G.B. Hinton 7058* (K, ARIZ, NA, US, MO). **Michoacan. Mpio. Arteaga:** Puente San Salvador, 630 m, 14 Mar 2005, *Provance 9919* (UCR, CIMI). **Mpio. Huetamo:** Arroyo Seco, *I. Garcia R. et al. 6873* (CIMI, UCR); Eréndira, 800 m, 5 Nov 1977, *J. Rzedowski 35495* (AAU, IEB). **Mpio. Tuzantla:** ca. km 68 carr. Zitácuaro-Tuzantla, 789 m, 16 Dec 2004, *I. Garcia R. et al. 6867* (CIMI, UCR); 9 km al NE de Tuzantla, 750 m, 20 Jun 1983, *J.C. Soto N. 5325* (MO); 10 km al NE de Tuzantla, 700 m, 12 Dec 1971, *F. Chiang et al. 547* (WIS, NA, SD, XAL).

2c. Diospyros aequoris Humb. & Bonpl. ex Willd. subsp. **chutlensis** M.C. Provance, I. García & A.C. Sanders, subsp. nov. (**Figs. 31, 32, 33, 39a, c**). Type. MÉXICO. Guerrero. Mpio. La Unión: Paraje "El Palomar," trayecto de terracería a Chutla, 10 m, 4 Dec 1993, *E. Guízar N. & L. Pimentel B. 3067* (holotype: IEB!; isotype: CHAPA).

Arbores et frutices multicaules a *Diospyros aequori* ssp. *aequori* similis sed differt foliis laminis tenuioribus, marginibus undulatis, venatione abaxiali subtiliore, et venatione secondaria in arcibus languidis terminanti.

Trees and multi-stemmed shrubs, 1.5–7.6 m tall; **trunk** somewhat smooth to fissured and scaly, the scales very thick, irregular, whitish-gray to grayish-beige; **branches** smooth to scaly or irregularly roughened; **stems** glabrous, or with some persisting wavy hairs in the second year, grayish-beige in life, the young stems densely short wavy-hairy, with sparse amounts ascending straight hairs up to 2 mm long near the shoot apex, the epidermis viscid, light dull orange to reddish-brown. **Petioles** 2–5 mm long, rugose, *margin* not or barely winged, dull orangish-red to gray magenta or light purplish-brown, rarely yellowish, densely hairy below, the hairs wavy or curved distally to wavy, off-white to tawny, densely hairy off-white to tawny wavy-hairy on the upper surface. **Lamina** flat or sometimes wavy in older leaves, but not typically wrinkled, chartaceous, 43–72 mm long, 18–34 mm wide, length to width ratio 1.5–2.5 : 1, elliptic to oblong-obovate, young leaves sometimes orbicular, the epidermis pale light green in life, *base* rounded to barely decurrent on the petiole, *margin* undulate, at least in life, sometimes slightly revolute, *apex* obtusely rounded; **lower lamina surface** glabrate to densely hairy, the hairs wavy or curved distally, < 1 mm long, upright, off-white to tawny, with sparse subappressed straight hairs ≤ 2 mm long, clavate glandular hairs often present, deciduous, leaving the brownish epidermis viscid, the stomatal apparatus subopaque, conspicuous; **upper lamina surface** with dense, tawny, wavy hairs, and occasional stellate hairs, the epidermis dark greenish-brown. **Venation** ± arcolanguid (the major lateral veins fading terminally, forming indistinct loops with superadjacent lateral veins); **midrib** prominent below, with more long straight hairs than the lamina surface, impressed basally on the upper surface, sparsely upright wavy-hairy, clavate glandular hairs often present, the epidermis dull yellow to light magenta; **lateral veins** 5–8 per side, irregularly spaced, angles of divergence from the midrib irregular, fine but prominent below, pubescent, the epidermis light dull orange to purplish-brown, barely raised above, the lamina-vein seams impressed; **3° veins** slightly raised below, inconspicuous above. **Male inflorescences and flowers** unknown. **Female inflorescences** unknown. **Female flowering calyx** (based on one immature fruiting calyx) densely tomentulose outside, *tube* thick, 2.3 mm long, ± 3 mm wide, *lobes* 7 mm long, 8 mm wide; **female corolla tube** 4 mm long, 3.5 mm wide, light reddish-cream sericeous inside, the hairs sparser in the basal 1/3, the epidermis dark reddish-brown; **female corolla lobes** ovate, 3 mm long, 1.8 mm wide; **Pistil** unknown. **Fruiting pedicels** 2.5–5 mm long, densely curly to wavy-hairy, bracts opposite, lanceolate, ± 2 mm long, concave. **Fruiting calyx** cupulate to explanate, outside minutely hairy, the hairs kinked to wavy, the epidermis shiny and viscid, dark reddish-brown, *tube* 3.5–6 mm long, dehiscent below the sinus for a short distance, the upper 1/2 becoming sparsely sericeous inside, glabrous basally, *lobes* obtuse, 4–7 mm long, 6.5–12 mm wide, vaguely pointed, laxly reflexed, tawny to reddish-brown sericeous inside with a broad intramarginal band. **Fruit** 2–2.3 cm in diameter, golden brown, sparsely pubescent, the hairs up to 2 mm long, translucent to tawny. **Seeds** 11–13 mm long, 6–6.5 mm radial depth, 4.5–5 mm wide.

The subspecies is endemic to the coastal plains of western Guerrero (Fig. 40). It typically grows on loamy or silty sand at the base of eroding slopes and on roadside embankments in dry tropical forest, and along the edges of planted fields. Known localities do not seem to be protected, but there are collections

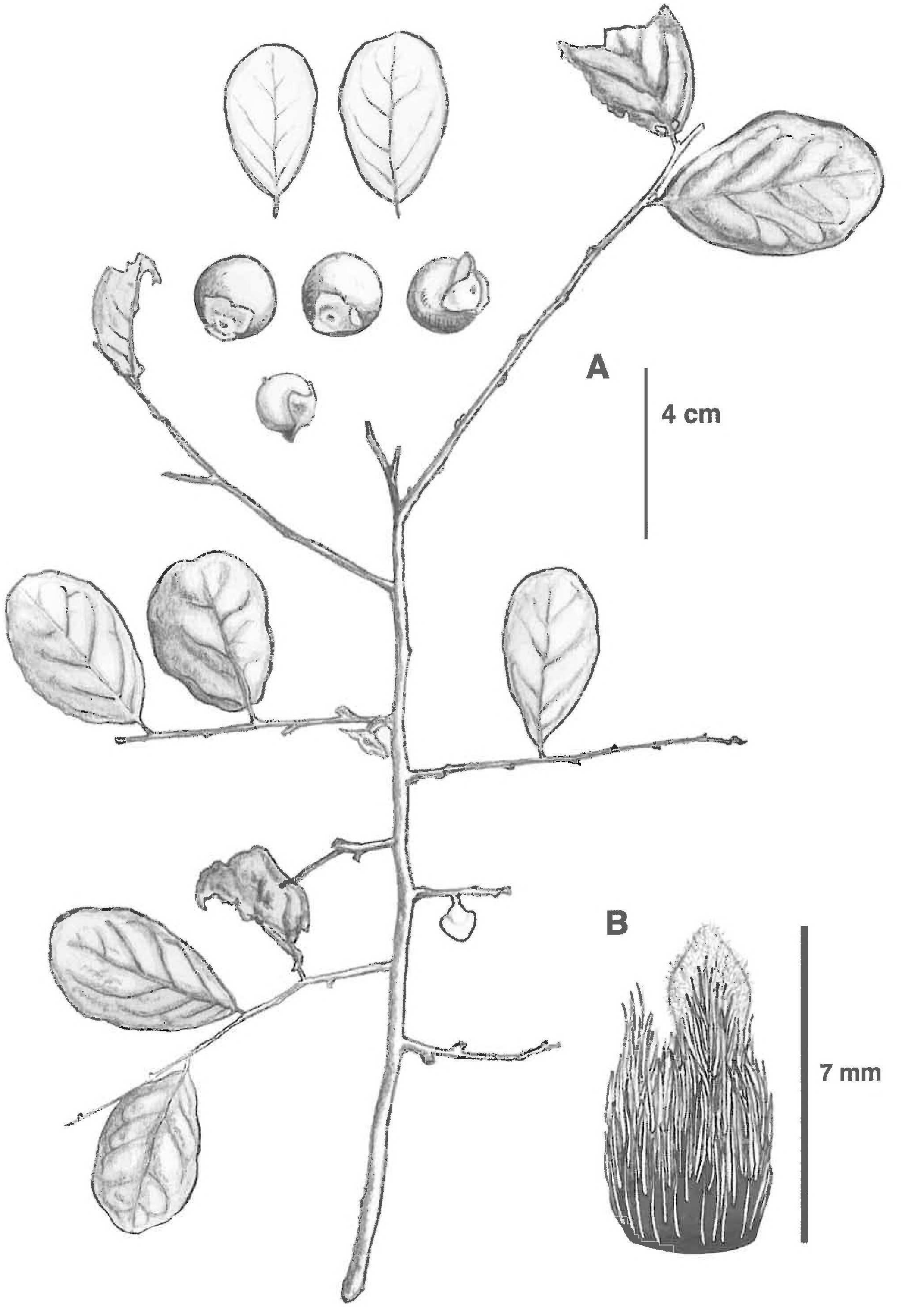

FIG. 31. **A.** *Diospyros aequoris* Standl. subsp. *chutlensis* M.C. Provance, I. García & A.C. Sanders, subsp. nov., based on the holotype from Paraje "El Palomar," trayecto de terracería a Chutla, Guerrero, Mexico (*E. Guízar N. & L. Pimentel B. 3067,* IEB). **B.** Female corolla of subsp. *chutlensis,* based on *G.B. Hinton et al. 14583* from Atoyac, Guerrero.

FIG. 32. Leaves of *D. aequoris* subsp. *chutlensis* from along dirt road between Hwy 200 and Chutla de Nava, Guerrero, with undulant margins.

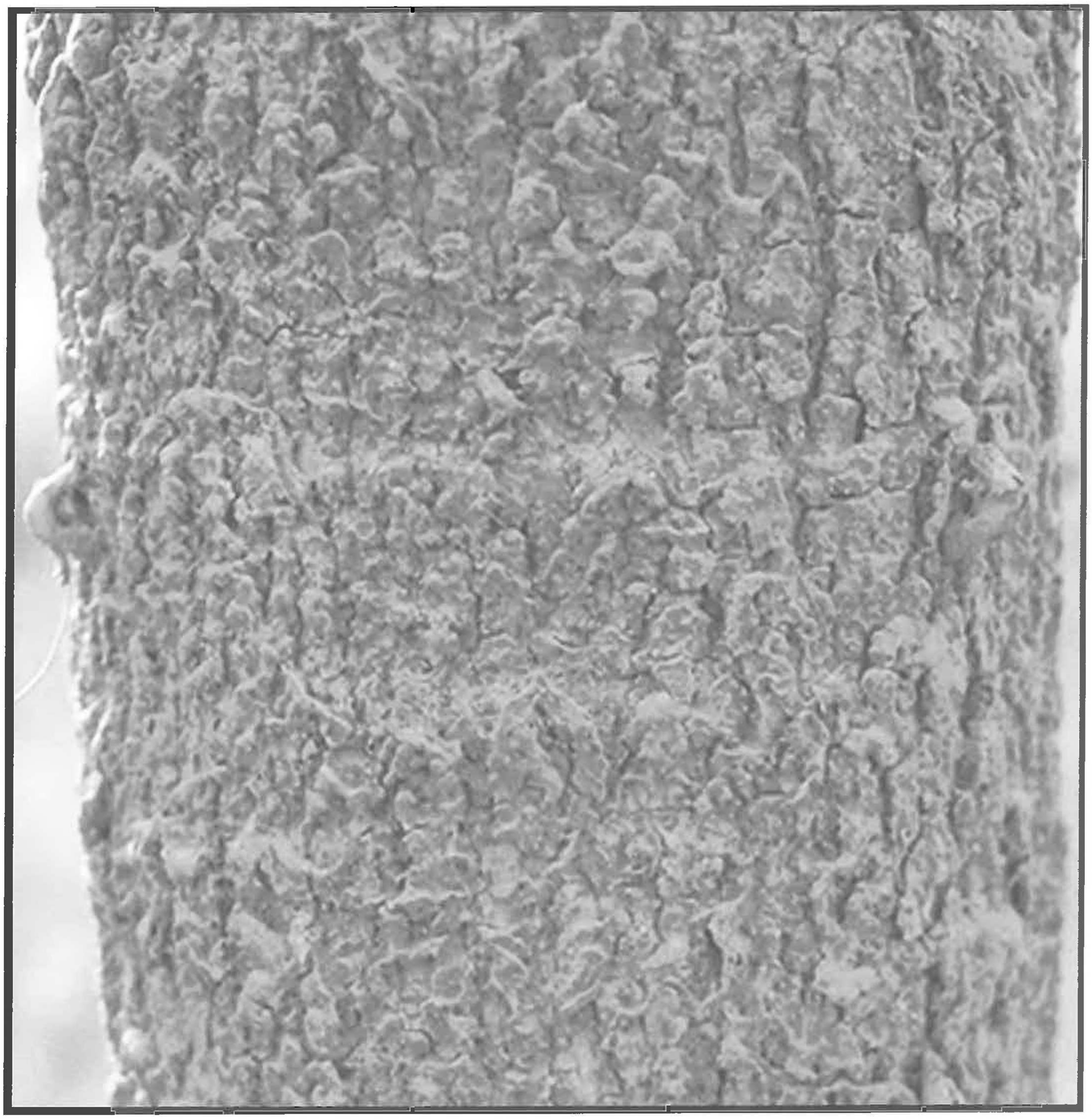

Fig. 33. Trunk (c. 9 cm dia.) of *D. aequoris* subsp. *chutlensis* from along dirt road between Hwy 200 and Chutla de Nava, Guerrero.

from Barbulillas, several hundred yards away from an ecological reserve in the vicinity of Ixtapa. Fonseca and Lozada-Pérez's (1993) description of "*Diospyros acapulcensis*" as one of the four most common shrubs in the halophytic vegetation zone along the coast southwest of Laguna de Coyuca may be in reference to this taxon. Although we have not seen specimens from their studies, based on the habitat and elevation, we suspect these reports represent *D. ae.* subsp. *chutlensis* or *D. salicifolia*. However, *Koch & Fryxell 82139* (US!, CHAPA!), collected near this locality represents *D. ae.* subsp. *chutlensis*. *Diospyros ae.* subsp. *martineziana* is separated by its smaller petioles, smaller lamina shape ratios, soft, fine, light colored, glossy abaxial lamina hairs, and brochidodromous venation. This taxon is quantitatively distinguished from *Diospyros salicifolia* by its shorter leaves with smaller lamina shape ratios (Table 1. characters 3, 7, 8). This subspecies is known to occur near, but not at Acapulco.

TABLE 1. Twenty-three leaf and fruiting inflorescence characters used in statistical analyses.

	Character	Abbrev.	Type
1.	lamina length	LL	leaf size
2.	lamina width	LW	leaf size
3.	lamina length : lamina width	LL:LW	leaf shape
4.	petiole length	ptL	leaf size
5.	lamina width at 0.25 length	LW1/4	leaf size
6.	lamina width at 0.75 length	LW3/4	leaf size
7.	lamina length : width at 0.25 length	LL:LW1/4	leaf shape
8.	lamina length : width at 0.75 length	LL:LW3/4	leaf shape
9.	lamina length : distance between four centermost lateral veins	LL:V	venation pattern
10.	lamina width at 0.25 length : width at 0.75	LW1/4:LW3/4	leaf shape
11.	lamina width at 0.25 : lamina width	LW1/4:LW	leaf shape
12.	lamina width at 0.75 : lamina width	LW3/4:LW	leaf shape
13.	fruiting pedicel length	pdL	infl. size
14.	fruiting sepal width	SW	infl. size
15.	fruiting sepal length	SL	infl. size
16.	fruiting calyx tube length	CL	infl. size
17.	fruiting sepal width : fruiting sepal length	SW:SL	infl. shape
18.	fruiting sepal width : fruiting calyx tube length	SW: CL	infl. shape
19.	fruiting sepal width : fruiting pedicel length	SW:pdL	infl. shape
20.	fruiting sepal length : fruiting calyx tube length	SL: CL	infl. shape
21.	fruiting sepal length : fruiting pedicel length	SL:pdL	infl. shape
22.	fruiting calyx tube length : fruiting pedicel length	CL:pdL	infl. shape
23.	fruiting calyx size (fruiting calyx tube length + fruiting sepal width + fruiting sepal width)	cx	infl. size

Representative specimens. **MEXICO. GUERRERO. Mpio. Acapulco de Juarez:** km 5.5 carr. Acapulco–Pie de la Cuesta, 60–160 m, 21 Oct 1982, *S.D. Koch & P.A. Fryxell 82139* (US, CHAPA); Punta Gorda, Laguna de Tres Palos, 10 m, 11 Oct 1988, *N. Diego 4920* (IEB). **Mpio. Átoyac de Alvarez:** Atoyac, [17°12'N, 100°26' W], 25-300 m, 30 Aug 1939, *G.B. Hinton et al. 14583* (UC, IJ, K). **Mpio. Coyuca de Benítez:** between Acapulco and Ixtapa, just N of El Zapote, 16 Jan 1983, *J.S. Miller et al. 461* (MO). **Mpio. José Azueta:** Punta Ixtapa, al W de Ixtapa Zihuatanejo, 30 m, 2 Apr 1991, *G. Castillo C. & P. Zamora C. 6276* (XAL); Ixtapa, Col. Barbulillas, 0.5 km N of Hotel La Costa, 25 m, 10 Mar 2005, *Provance 10020A* (UCR, CIMI) and *Provance 10020B* (UCR, CIMI). **Mpio. La Unión de Isidoro Montes de Oca:** Felicianos, road N from Hwy 200, 45 m, *Provance 9981* (UCR, CIMI); road N from Hwy 200 going towards Chutla, 61 m, *Provance 9923* (UCR, CIMI); Joluta, several km N of Hwy 200, 61 m, *Provance 9930* (UCR, CIMI); vicinity of Coyuquila and La Salada, along Hwy 200, 25 m, *Provance 9933* (UCR, CIMI); Japoncito, dirt road on N side of Hwy 200, 26 m, *Provance 9932* (UCR, CIMI); 46 mi NW of Zihuatanejo, 7 Mar 1979, *C.D. Johnson 667-79* (MO).

2d. Diospyros aequoris Standl. subsp. **martineziana** (Standl. ex Leavenworth) M.C. Provance, I. García & A.C. Sanders, comb. et stat. nov. (**Figs. 34, 38d**). BASIONYM: *Diospyros martineziana* Standl. ex Leavenworth, Amer. Midl. Naturalist 36:184. 1946. TYPE: MEXICO. MICHOACAN: Tancitaro Region, Acahuato, above 2500 ft, 20 Aug 1941, *W.C. Leavenworth & H. Hoogstraal 1735* (HOLOTYPE: F).

Trees, sometimes shrubs, 1.2–8 m tall; **trunk** up to 30 cm in diameter, bark somewhat smooth (not slick), with scattered checked regions, sometimes irregularly patchy, light to dark gray; **stems** scurfy to glabrous and very dark or castaneous, the young stems densely hairy, the hairs slightly wavy to curly, spreading to ascending, colorless to white, clavate glandular hairs sometimes present. **Petioles** 2–3(–5) mm long, glabrous to densely straight to slightly wavy subappressed hairy, pubescent above. **Lamina** chartaceous, orbicular, oblong or obovate, 19–61(–65) mm long, 13–40 mm wide, sapling leaves 70–87 mm long, 40–54 mm wide, length to width ratio 1.2–1.5 : 1, *base* rounded to subcordate, slightly decurrent on the petiole, *margin* flat, *apex* rounded to obtuse, sometimes retuse, sometimes subacute; **lower lamina surface** moderately to densely hairy, the hairs wavy to straight, subappressed to upright, soft, fine, glossy, white to gold, clavate glandular hairs sometimes present, the epidermis, yellowish to dark green; **upper lamina surface** sparsely

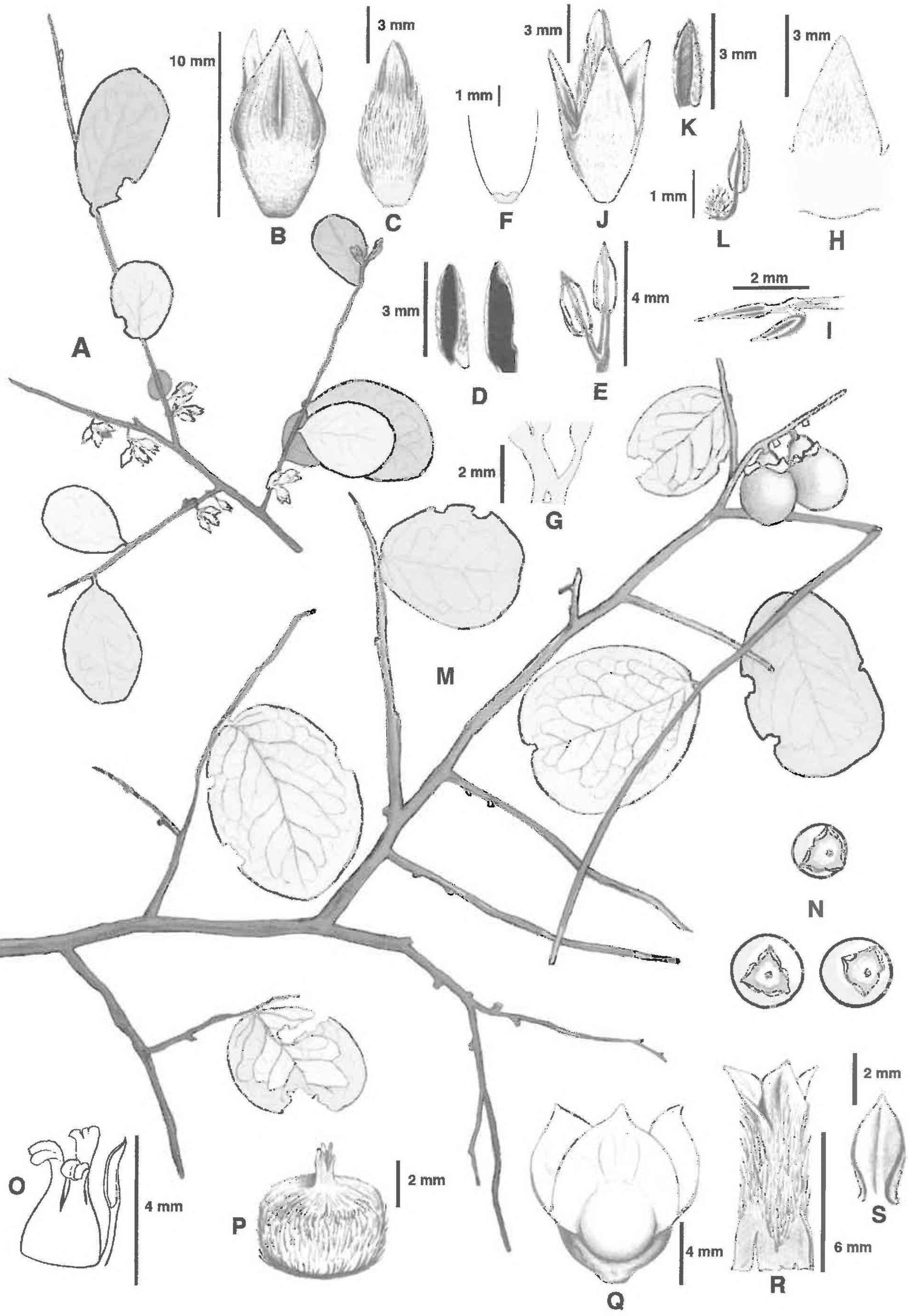

Fig. 34. *Diospyros aequoris* subsp. *martineziana*. **A–E.** Based on *M.C. Provance & I. García R. 9393* (UCR). **A.** Stem with young growth and male flowers. **B.** Male flower with keeled calyx lobe. **C.** Male corolla. **D.** Male corolla lobes. **E.** Geminate stamens. **F–I.** Based on *M.C. Provance & I. García R. 9394* (UCR). **F.** Male corolla glabrous zone. **G.** Lateral fusion of filaments. **H.** Adaxial surface of male flowering calyx. **I.** Geminate stamens. **J–L.** Based on *J.C. Soto N. & E.M. Martínez 4189*. **J.** Male corolla. **K.** Male corolla lobe. **L.** Pistillode and stamen with filament inserted on the receptacle. **M–N.** Based on *I. García R. & C. Conrado 6989* (UCR). **M.** Fruiting branchlet. **N.** Fruiting calices. **O.** Pistil and staminode (vestiture not illustrated) of flower type I, based on *M.C. Provance & I. García R. 9396A* (UCR). **P–S.** Based on *M.C. Provance & I. García R. 9392* (UCR). **P.** Pistil of flower type II. **Q.** Female flower. **R.** Female corolla. **S.** Female corolla lobe.

to densely hairy, the hairs uniformly curved to wavy, ascending to upright, soft, fine, white to gold, the epidermis olive to dark green, hair bases raised and nearby epidermal cells enlarged. **Venation** brochidodromous, yellow to chartreuse; **midrib** prominent below, narrow, with spreading, straight to slightly wavy hairs above; **lateral veins** (3–)4–6(–7) per side, fine but prominent below, connecting with superadjacent laterals inward from the margin, sparsely hairy, barely impressed to barely raised above (± obscure); **3° veins** very fine below, obscure above. **Male inflorescences** solitary (1–)3–4(–6)-flowered cymes, densely cream to yellowish-orange tomentulose to wavy-hairy; **peduncles** 0.5–3 mm long; **pedicels** 0.5–2 mm long. **Male flowering calyx** sometimes slightly winged, moderately to densely white to yellowish velutinous-pubescent, the hairs sometimes subappressed with tomentulose undercoat, epidermis viscid *tube* 2.5–3.5 mm long, 3.8–4 mm wide, glabrous inside, *lobes* acute, (3.5–)5.5–6(–7) mm long, (3–)4–4.5(–5.5) mm wide, sometimes keeled, the nerves sometimes obvious, densely hairy inside, the intramarginal band width variable; **male corolla tube** 4.5–6 mm long, 3–4 mm wide, sericeous outside, with 3 pale pink 0.5–0.8 mm long shield-shaped glabrous basal regions; **male corolla lobes** lance-ovate to elliptic, 3–3.5 mm long, 1.2–2.5 mm wide. **Stamens** 10–12; **filaments** adnate to the base of the corolla or inserted on the receptacle, 2–2.5 mm long, narrowed distally, free, geminate or joined laterally, rarely in threes; **anthers** lance-ovate, 2–2.5 mm long, sometimes rostrate. **Female inflorescence** densely hairy, bracts narrowly triangular, 1.0–1.3 mm long. **Female flowers** apparently dimorphic (types I and II below, both types can be found in one individual); **female flowering calyx** densely tomentulose outside, with some longer, straight to slightly wavy, ± ascending, light gold hairs, *tube* half-globose, 5–6 mm long, 7 mm wide, the upper 1/2 densely hairy inside, lower 1/2 glabrate with a few reddish glandular hairs, *lobes* 7–8 mm long, 7–8 mm wide, acuminate, the nerves prominent, densely hairy inside with a broad intramarginal band; **female corolla tube** 6 mm long, 3.3 mm wide, with 3 shield-shaped 3.5 mm long glabrous basal regions: **flower type I corolla tube** basal regions pinkish, ± overlapping; **flower type II corolla tube** basal regions dark red, not or barely overlapping; **female corolla lobes** rhombic to ovate, 4 mm long, 2 mm wide; **flower type I ovary** ovoid, minutely cream sericeous; **flower type II ovary** shaped like a barrel, glabrous to scantily hairy, epidermis golden; **flower type I styles** 3, free, arching outward; **flower type II styles** 3, in a fused column; **stigmas** bifid. **Fruiting pedicels** 2–4 mm long, bracts slender, 1.8–2 mm long, about 0.3 mm wide, conduplicate. **Fruiting calyx** shallowly rotate to cupuliform, tomentulose to wavy-hairy outside, much of the vestiture including the longer hairs, deciduous in age, sometimes persisting on the conspicuously viscid, epidermis *tube* 5–5.5 mm long, densely hairy inside, *lobes* spreading, obtuse to rounded, 3–8 mm long, 8.5–10.5 mm wide, the margins usually revolute. **Fruit** globose, subglobose or obovoid, 2–2.3 cm in diameter, glabrous or sparsely hairy, the hairs straight to slightly wavy, fine, ascending, white to golden, clavate glandular hairs sometimes present, epidermis glaucous, pruinose, scintillant, tending to separate from the remainder of the fruit upon drying, light grayish-yellow to golden brown, mature fruit light green in life. **Seeds** 13–14 mm long, 6 mm radial depth, 5.5 mm wide.

This subspecies grows in dry deciduous forest of the Apatzingan Valley, Michoacan, between 320 and 700 m (Fig. 40). Its occurrence has not been documented for any protected area. It is an occasional tree at the type locality on the slopes of Acahuato, north of Apatzingan, Michoacan, where it is sometimes spared adjacent to milpas to produce shade for workers (pers. obs).

Representative specimens: **MÉXICO. Michoacan: Mpio. Apatzingan:** Acahuato, 671 m, 2 Jul 2004, *M.C. Provance & I. Garcia R. 9392, 9393, 9395, 9396A, 9396B, 9394* (CIMI, UCR); Acahuato, 750 m, 17 Feb 2005, *I. Garcia R. & C. Conrado 6989, 6983* (CIMI, UCR); above Apatzingan, 2000 ft, 13 Aug 1941, *W.C. Leavenworth & H. Hoogstraal 1502* (MO, ILL), same location, *1490* (MO, ILL), same location, *1494* (MO, ILL); Mt. Apatzingan, 2000 ft, 20 Aug 1941, *W.C. Leavenworth & H. Hoogstraal 1728* (MO). **Mpio. Huetamo:** En Pataseo [Patasco], 6 km al E de Quetzería, 300 m, 18 Jul 1982, *J.C. Soto N. & E.M. Martínez 4189* (XAL, CHAPA, MO, ILL). **Mpio. La Huacana:** Sierra Las Cruces, ca. 6.5 km (by air) west-southwest of Los Ranchos, 600 m, 6 Dec 2003, *Steinmann 3911* (UCR). **Mpio Parácuaro:** "Paso de Yeguas" [Crucero de las Yeguas], 17 km a W de Cuatro Caminos, 250 m [± 320 m], 18 Oct 1982, *R. Torres C. 1541* (CAS).

2e. Diospyros aequoris Standl. subsp. **rekoi** (Standl.) M.C. Provance, I. García & A.C. Sanders, comb. et stat. nov. (**Figs. 35, 38a**). Basionym: *Maba rekoi* Standl. Contr. U.S Natl. Herb. 20:193. 1919. Type: MEXICO. Oaxaca. [Mpio.

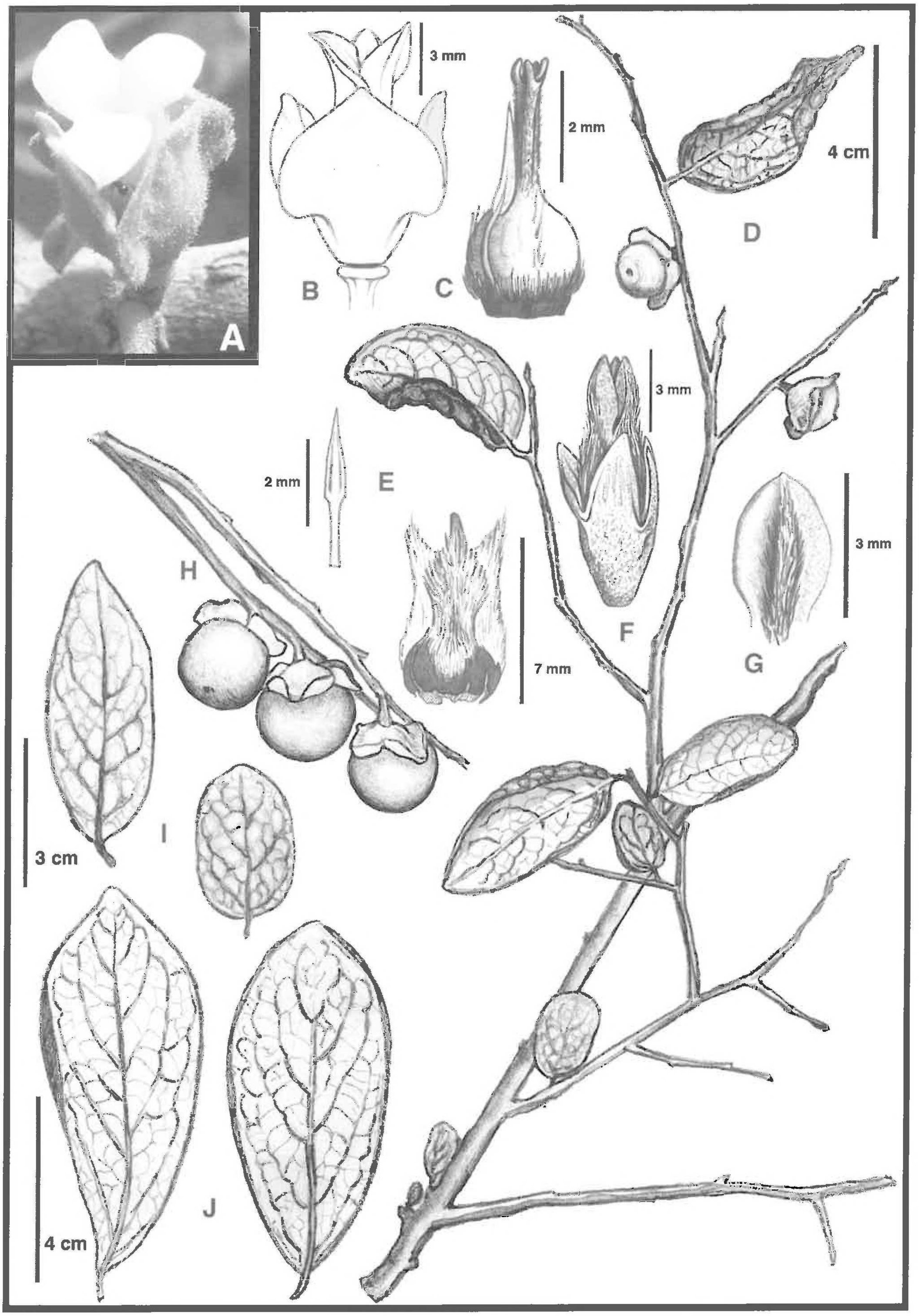

Fig. 35. *Diospyros aequoris* subsp. *rekoi*. **A.** Female flower photographed at Tahueca, Oaxaca. **B.** Diagram of female flower. **C.** Pistil with staminode. **D.** Branchlet with immature fruit. **E.** Female corolla and staminode. **F.** Male corolla. **G.** Male corolla lobe. **H.** Branchlet with fruit. **I.** Leaves (adaxial surface). **J.** Leaves (abaxial surface). **B–C, G.** Based on *T.B. Salvato & M.C. Provance 247* (UCR). **D, H–I.** Based on *T.B. Salvato & M.C. Provance 246* (UCR). **E, I.** Based on *T.B. Salvato & M.C. Provance 293* (UCR). **F.** Based on *T.B. Salvato & M.C. Provance 244* (UCR).

San Pedro Pochutla]: Puerto Angel, [15°40'N, 96°29'W, 1 m], 28 Sep 1917, *B.P. Reko 3429* (HT: US-842523). *Diospyros portus* Standl. Publ. Carnegie Inst. Wash. 461(4):80. 1935.

Not *Diospyros rekoi* Standl., J. Wash. Acad. Sci.17: 527. 1927.

Shrubs, rarely trees, 1–4(–12) m tall, sometimes with multiple stems from root and crown sprouts; **trunk** somewhat smooth (not slick) to checked, the bark whitish with gray to gold patches; **stems** glabrous, sometimes hispidulous or with longer desiccated hairs in the 2nd year, young stems densely puberulent, with some additional longer, spreading to ascending hairs. **Petioles** (3–)4–6(–7) mm long, glistening, dark, reddish, densely minutely wavy-hairy on the lower surface, the hairs sparser and longer above. **Lamina** subcoriaceous, oblong or elliptic to obovate, (40–)50–90(–100) mm long, 16–35(–45) mm wide, the length to width ratio 2.2–2.8 : 1, *base* broadly rounded to the petiole, *margin* revolute, *apex* broadly to obtusely rounded (revolute lamina margins sometimes forming a false point); **lower lamina surface** moderately velutinous to wavy-velutinous, the hairs ascending to upright, clavate glandular hairs often present, deciduous, leaving the epidermis conspicuously viscid, the stomatal apparatus opaque and conspicuous to translucent; **upper lamina surface** wrinkled when mature, velutinous to wavy-velutinous. **Venation** brochidodromous; **midrib** prominent below, ascending velutinous, impressed above, velutinous to wavy-velutinous, clavate glandular hairs often present; **lateral veins** 4–8 per side, prominent below, impressed above; 3° veins prominent below, impressed above; 4° veins sometimes darkened below. **Male inflorescences** 1–3-flowered cymes, hirsutulous; **peduncles** 1–3 mm long; **pedicels** 0.3–2 mm long, bracts linear-lanceolate, 2–3 mm long, conduplicate. **Male flowering calyx** densely puberulent, the epidermis viscid, *tube* 3–4 mm long, 3–3.5 mm wide, glabrate inside, some scattered minute hairs in the lower 1/2, *lobes* acute, (3.5–)5–6 mm long, 3–5 mm wide, glabrous to sparsely puberulent inside, the intramarginal band somewhat narrow; **male corolla tube** 4.8–5.5 mm long, 3 mm wide, mostly sericeous outside, but basal 0.3–0.8 mm glabrous; **male corolla lobes** oblong, ovate or rhombic, 3–4 mm long, 2 mm wide; **Stamens** (11–)12; **filaments** adnate to the tube near the base, irregularly or vaguely in two tiers, or inserted on the receptacle, 2 mm long, sometimes subgeminate; **anthers** lanceolate to oblong, 2–2.4 mm long, sometimes minutely lobed basally on each side of the connective ('eared'), sometimes apiculate. **Female inflorescences** wavy-hirsutulous with orangish ascending hairs, bracts linear-lanceolate, 2–3 mm long, conduplicate. **Female flowering calyx** campanulate, straight to wavy-hairy, the hairs upright to ascending, orangish, *tube* cupulate, 2.5–3 mm long, 5 mm wide, *lobes* obtusely rounded, 5.5–6 mm long, 6.5 mm wide, barely acuminate; **female corolla tube** 5.5–7.5 mm long, 3.5–4 mm wide, exterior sericeous nearly to the base; **female corolla lobes** ovate to rhombic, 3.3-4 mm long, 2.5 mm wide; **ovary** globose to somewhat conical, ± 2 mm in diameter, usually glabrous, sometimes with 3 rows of long hairs running from the base of the ovary to the base of the style column; **styles** 3, column ± 2.5 mm long; **stigmas** bifid, ± 0.5 mm long, somewhat spreading; **staminodes** 3(–5), opposite to the petals, flat, the sterile anther narrowly lanceolate, 2 mm long, the filament 2 mm long, adnate to the base of the corolla for 0.5–0.8 mm. **Fruiting pedicels** 4–8(–12) mm long, often glabrate. **Fruiting calyx** rotate, glabrate to sparsely straight to wavy-hairy, the epidermis dark brown and conspicuously viscid, *tube* 4.5–6.5 mm long, hairy inside to the base, *lobes* 5–8 mm long, 11–14 mm wide, sericeous inside with a broad intramarginal band. **Fruit** 1.5–2.2 mm in diameter, epidermis reportedly yellow when mature. **Seeds** unknown.

This subspecies is endemic to the coastal region of Oaxaca (Fig. 40). It is common on sandy mesas with littoral scrub near the beach, and on rocky seaside cliffs where it tolerates at least small amounts of salt-spray. It also occurs a few kilometers inland on steep rocky slopes with dry tropical forest. Saplings are sometimes very common along disturbed sandy roads near the beach. This subspecies forms intermediates with *D. ae.* subsp. *tehuantepecensis* several kilometers east of Bahias de Huatulco, but can generally be distinguished from it by its longer and wider lamina, longer petioles, larger calyx including wider fruiting sepals, longer fruiting pedicels, and longer tube.

Representative specimens: **MEXICO. Oaxaca. Mpio. San Pedro Mixtepec:** Puerto Escondido, 22 Sep 1982, *R. Cedillo T. & R. Torres C. 1813* (MO, XAL). **Mpio. San Pedro Pochutla:** Tahueca, 10–15 m, 3 Aug 2003, *T.B. Salvato & M.C. Provance 244, 245, 246, 247* (UCR).

Mpio. Santa María Huatulco: Cerro San Antonio, Bahia de San Agustin, 50–60 ft, *T.B. Salvato & M.C. Provance 293* (UCR). **Mpio. Santa María Tonameca:** Playa Agua Blanca, 35 m, 4 Aug 2003, *T.B. Salvato & M.C. Provance 363, 366* (UCR).

2f. Diospyros aequoris Standl. subsp. **tehuantepecensis** M.C. Provance, I. García & A.C. Sanders, subsp. nov. (**Figs. 36, 37a–i, 39b**). TYPE: MEXICO. OAXACA. Mpio. Tehuantepec: Mixtequilla, senda a las ruinas del Cerro Guiengola, 16°22'55.4"W, 95°18'27.3"W, 300 m, 6 Aug 1994, *J.L. Panero & J.I. Calzada 4490* (HOLOTYPE: IEB-48849!; ISOTYPES CAS!, TEX!).

Arbores et frutices a *Diospyros aequori* ssp. *aequori* similis sed differt laminis foliorum griseoribus plerumque angustioribus ad 1/4 et 3/4 longitudinem, infra venatione cremea vel magentea vel coloribus ambabus maculata.

Trees or shrubs, 2–5 m tall; **trunk** unknown; **stems** glabrous to pulverulent or scurfy, the young stems pilosulose to villosulous, with some longer slightly wavy ascending reddish-orange hairs near the shoot apex. **Petioles** 2–4(–5) mm long, hairs similar to young stems, rugose below and sometimes above, epidermis magenta to yellowish or cream, sometimes variously striated. **Lamina** chartaceous to subcoriaceous, elliptic or oblong, sometimes obovate, rarely oblanceolate, 29–56(–67) mm long, 12–24(–27) mm wide, length to width ratio (1.6–)2.1–2.6 **:** 1, *base* rounded to the petiole, *margin* sometimes revolute near the base, *apex* obtusely rounded, sometimes acutely; **lower lamina surface** hairs moderate to dense, straight to wavy, ascending to subappressed, clavate glandular hairs often present, the epidermis usually light gray, the stomatal apparatus opaque, white, and conspicuous; **upper lamina surface** usually wrinkled, villous, clavate glandular hairs often present, the epidermis densely papillose. **Venation** brochidodromous to arcolanguid, below off-white to gray pilosulose to villosulous, the epidermis cream to magenta or speckled with both colors; **midrib** prominent below, impressed above except basally where slightly raised, densely villous, the epidermis yellow orange; **lateral veins** 5–7 per side, prominent below, slightly impressed above; **3° veins** raised below, slightly impressed above. **Male inflorescences** 3-flowered cymes; **pedicels** 1–2 mm long, densely pubescent. **Male flowering calyx** densely pubescent to wavy-hairy outside, hairs ascending, off-white, *tube* urceolate, 4 mm long, 3.5–4 mm wide, weakly winged, glabrous inside, *lobes* triangular, 4–5 mm long, 3–3.2 mm wide, ascending to slightly spreading, glabrous inside with a narrow intramarginal band; **male corolla tube** 5.5–6 mm long, 3 mm wide, the upper 1/2 sericeous outside, lower 1/2 with 3 shield-shaped glabrous basal areas, ± 1.8 mm long, bordered distally by minute curly ascending hairs; **male corolla lobes** rhombic, 3 mm long, 1.8–2 mm wide, sometimes involute basally. **Stamens** 12; **filaments** adnate to the base of the corolla in a single tier, rarely inserted on the receptacle, 2 mm long; **anthers** lanceolate, 2.3 mm long. **Female inflorescences** densely pubescent. **Female calyx** densely minutely sericeous outside, with sparse longer, wavy, ascending to spreading hairs, *tube* shallow-cupulate, 1.5 mm long, 4 mm wide, glabrate inside, *lobes* obtusely rounded, 6–7 mm long, 7–7.5 mm wide, densely hairy inside with a broad intramarginal band; **female corolla tube** 4.5 mm long, 3 mm wide, similar to male corolla tube, the glabrous basal regions 3 mm long, 2.2 mm wide; **female corolla lobes** rhombic, 3.5 mm long, 2 mm wide; **ovary** depressed-globose, 2 mm long, 3 mm wide, cream sericeous; **styles** 3, upright, not fused, 1.8 mm long, minutely sericeous abaxially, white tomentulose adaxially; **stigmas** 3, bifid; **staminodes** 3, the filaments adnate to the corolla base, 1.5–2 mm long, the sterile anther narrowly lanceolate, 1.5 mm long. **Fruiting pedicels** 2.5–6.5(–8) mm long, densely ascending-pubescent. **Fruiting calyx** explanate, densely puberulent outside, hairs cream to orange; *tube* (3–)4–5(–7) mm long, *lobes* broadly obtuse, (3.5–)4–8 mm long, (7–)8.5–12.5 mm wide, spreading to reflexed. **Fruit** globose, 1.5–2.5 cm in diameter, glabrous to sparsely puberulent, the hairs minute, straight, appressed to ascending, epidermis amber to dark yellow, green in living material when mature. **Seeds** 11–12.5 mm long, 8 mm radial depth, 5–6 mm wide.

This subspecies occurs in dry tropical forests, between 50 and 1100 m, in the southwest part of the Isthmus of Tehuantepec, Oaxaca (Fig. 40). It has been described as frequent at three sites with limestone substrates but has also been reported from sandy soils and disturbed sites. The occurrence of this taxon on Cerro Guiengola is significant because dry tropical forests of this region are considered high in quality, and have consequently been recommended for formal conservation following a study by Gordon et al. (2004). The species forms hybrids with *D. ae.* subsp. *rekoi* in the vicinity of Tehuantepec and in coastal regions near Salina Cruz, and in the Municipio of Santiago Astata.

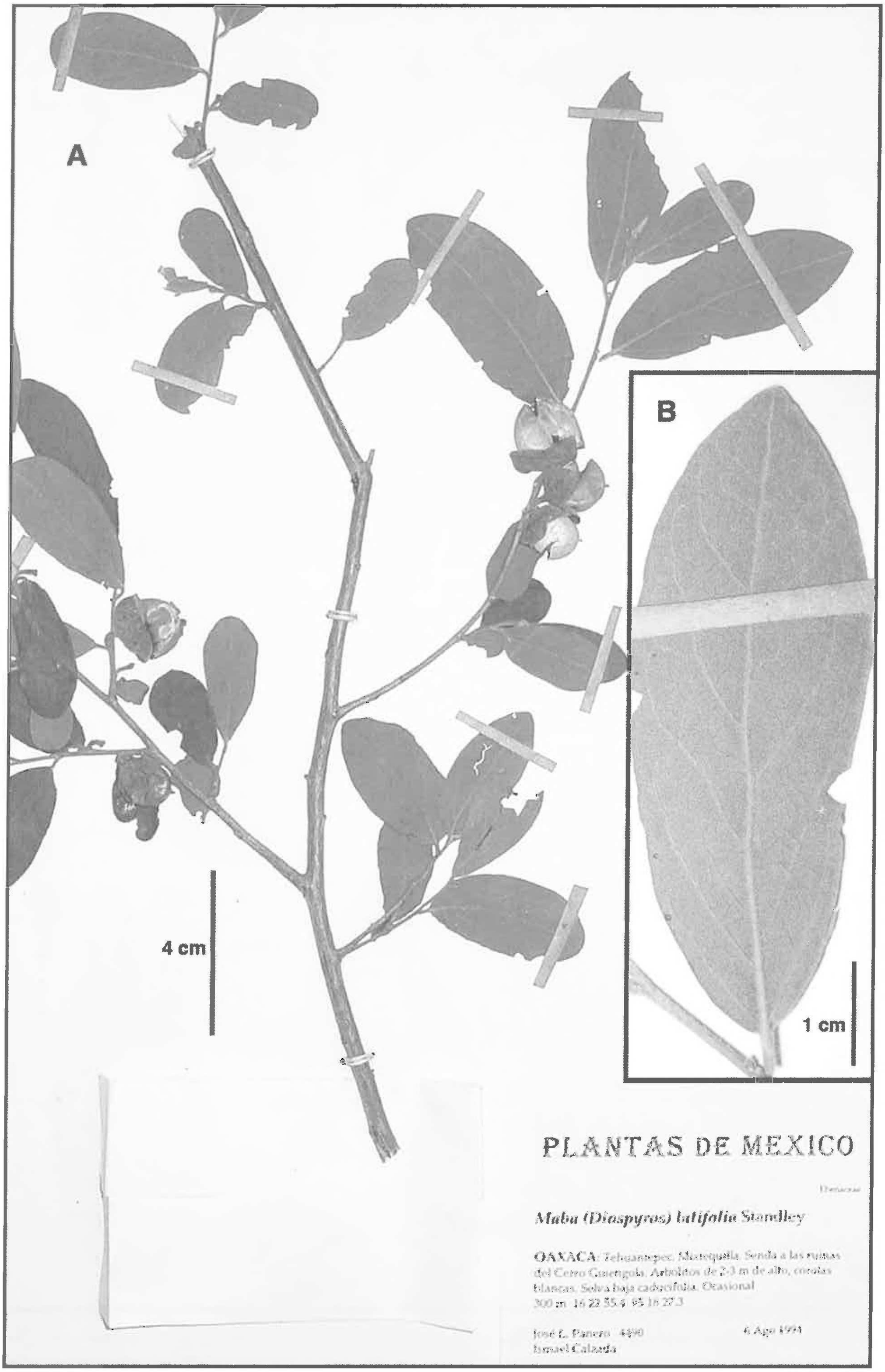

FIG. 36. Holotype of *D. aequoris* Standl. subsp. *tehuantepecensis* M.C. Provance, I. García & A.C. Sanders, subsp. nov. from Mixtequilla, Oaxaca (*J.L. Panero & J.I. Calzada 4490,* IEB-48849). **A.** Fruiting branchlet. **B.** Leaf (abaxial surface).

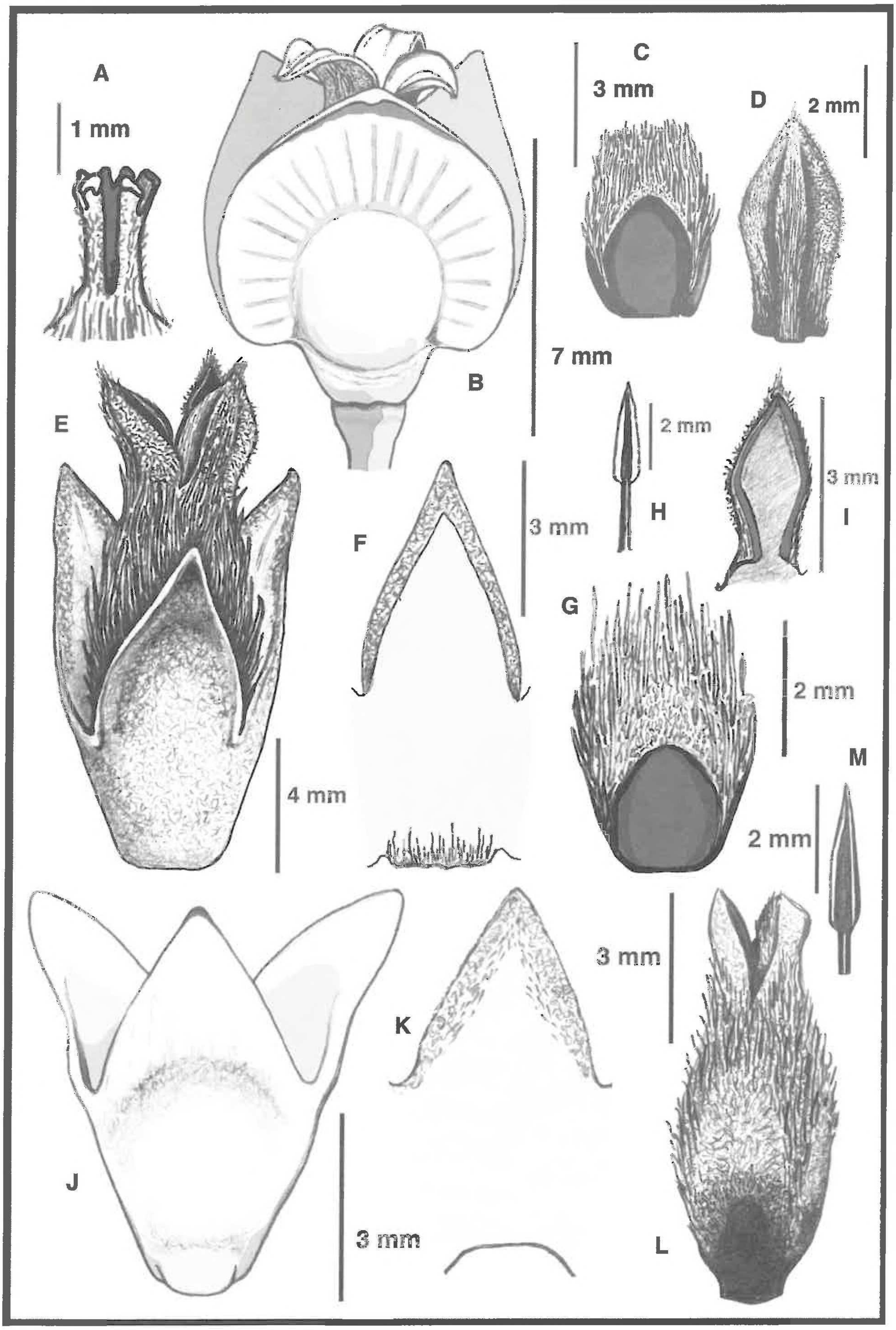

FIG. 37. *Diospyros aequoris* Standl. **A–I.** subsp. *tehuantepecensis*. **A–D.** Based on *J.L. Panero & J.I. Calzada 449* (CAS). **A.** Styles and stigmas. **B.** Female flower. **C.** Female corolla tube. **D.** Female corolla lobe (abaxial view). **E–I.** Based on *J. Rzedowski 33065* (MOU). **E.** Male flower. **F.** Adaxial surface of male calyx. **G.** Male corolla tube (adaxial view). **H.** Stamen. **I.** Male corolla lobe. **J–M.** subsp. *balsensis*, based on *G.B. Hinton 3959* (K) from Bejucos, Mexico. **J.** Male calyx. **K.** Adaxial surface of male flowering calyx. **L.** Male corolla. **M.** Stamen.

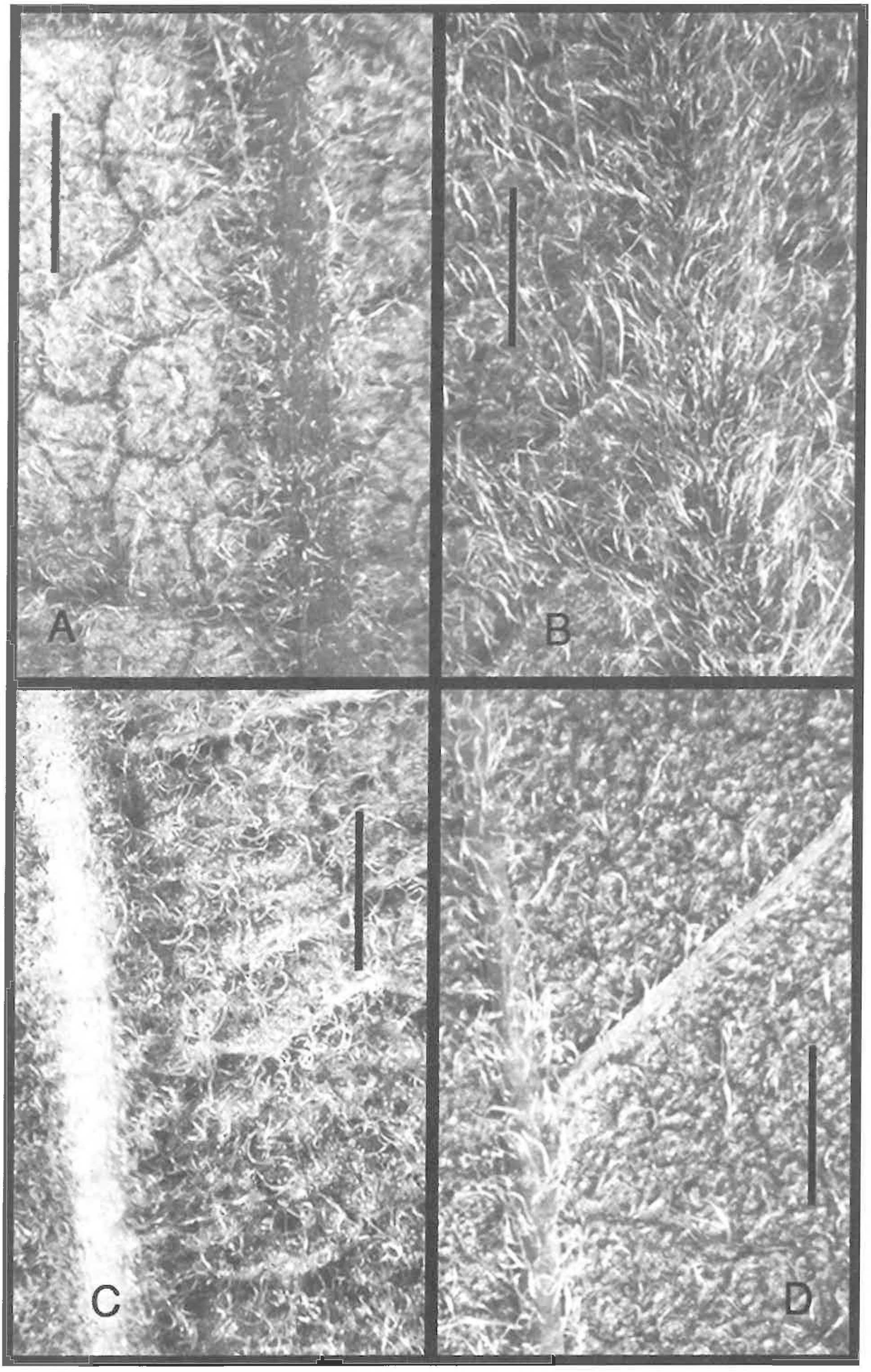

FIG. 38. Abaxial leaf vestiture *D. aequoris*, including midrib (scale = 1 mm). **A.** subsp. *rekoi* (*T. Salvato & M.C. Provance 487*, UCR). **B.** subsp. *aequoris* (*M.C. Provance et al. 9607*, UCR). **C.** subsp. *balsensis* (*M.C. Provance 9919*, UCR). **D.** subsp. *martineziana* (*M.C. Provance & I. Garcia R. 9396B*, UCR).

Representative specimens. **MEXICO. Oaxaca. Mpio. Guevea de Humboldt:** Cerro de Picacho, Jul 1914, *C.A. Purpus 7444, 7176* (MO). **Mpio. Ixtepec:** Cerro Blanco por la carretera Juchitán–Ixtaltepec, 200 m, 15 Feb 1982, *J.I. Calzada & J. Elizondo 8508* (XAL). **Mpio. Magdalena Tequisistlán:** 8 km al SW de La Pajima, 285–330 m, 29 Aug 1994, *G. Flores-Franco & J.I. Calzada 3621* (NLU, ARIZ). **Mpio. Magdalena Tlacotepec:** 4 km del ojo de agua de Tlacotepec hacia la Ollaga, 260 m, 26 Sep 1984, *R. Torres C. 6277* (MO). **Mpio. San Pedro Huamelula:** Playa Grande, 2.1 km al E, 50 m, 31 Jul 2000, *S. Salas M. 3213* (IEB). **Mpio. Santa Maria Jalapa del Marqués:** Rancho Ricardo, al N. de Buenos Aires, entrando por Hierba Santa, 12 Sep 1985, R. Torres C. & C. Martínez 7312 (MO). **Mpio. Santiago Lachiguirí:** Aproximadamente 10 km al NE de la cortina de la Presa Benito Juárez, camino de terraceria a Santiago Lachiguirí, 100 m, 24 Aug 1994, *G. Flores-Franco 3556 & J.I. Calzada* (ARIZ). **Mpio. Santo Domingo Ingenio:** 10 km al NE de La Ventosa, 2 Dec 1980, *R. Cedillo T. & D. Lorence 503* (ILL). **Mpio. Tehuantepec:** 22 km WNW de Tehuantepec, sobre la carr. a Oaxaca, 200 m, 22 May 1975, *J. Rzedowski 33065* (MOU); 5 km al SW de Tehuantepec, 40 m, 28 Jun 1982, *R. Torres C. & R. Cedillo T. 684* (CHAPA, MO); al O de Buenos Aíres, 15 km al O de Tehuantepec, 400 m, 5 Feb 1988, *C. Martínez R. 1288* (IEB); Piedra de Cal, 5 km al NO de Tehuantepec, 50 m, 18 Feb 1984, *P. Tenorio L. & R. Torres C. 5480* (MO, CHAPA); "Rancho Lizet," 6.3 km al SW de la entrada a Buenos Aíres, 190 m, 26 Mar 1984, *R. Torres C. & C. Martínez R. 4787* (MO, CHAPA); Cerro Guiengola, 1110 m, 27 Nov 1983, *R. Torres C. 4194* (CHAPA); Cerro Pozo Zorillo, entrando por Las Pilas, 8 Feb 1988, *C. Martinez R. 1297* (IEB); 20 km al O de Tehuantepec, entrando por Las Pilas, 5 Jan 1988, *C. Martínez R. 1158* (MO).

3. Diospyros salicifolia Humb. & Bonpl. ex Willd. Sp. Pl. Editio quarta 4:1112. 1806 (**Figs. 1, 2c, 39d, 41, 42, 43**). *Maba salicifolia* (Humb. & Bonpl. ex Willd.) Hiern, Trans. Cambridge Philos. Soc. 12:129. 1873. Type: MEXICO. Guerrero: near Acapulco, no date, *Humboldt & Bonpland s.n.* (holotype: B-W-19250-01, digital images!).

Diospyros albens C. Presl, Reliq. Haenk. 2:62. 1835. *Macreightia albens* (C. Presl) A. DC., Prodr. (DC.) 8:221. 1844. *Ebenus albens* (C. Presl) Kuntze, Revis. Gen. Pl. 2:408. 1891. Type. MEXICO. Guerrero: "Habitat ad portum Acapulco Mexicanorum," date unknown, *T. Haenke s.n.* (holotype: W-31942, as photo F!).

Trees, 1.5–6 m tall, facultatively deciduous; **trunk** unknown; **wood** unknown; **mature stems** terete, half-netted, glabrate sometimes black gland-dotted, epidermis tan; **2nd year stems** similar to mature stems; **1st year stems** quadrangular, becoming terete, moderately hairy, the hairs usually minute, thick, appressed, fluid-filled (the hairs throughout the plant are mostly simple glandular hairs, likely translucent in life, and the color of hairs in herbarium specimens is due to darkening of a fluid in the lumen), associated with glandular punctae, rarely some longer wavy subappressed hairs present near the tip of the growing shoot, lenticels narrowly elliptic, few in number, *bud scales* deeply concave, triangular, 1.5–2 mm long, moderately to densely hairy, the hairs strongly appressed, similar to those on the young stems, glandular punctate, sometimes with minute clavate glandular hairs. **Leaves** alternate, simple, entire, closely spaced on new growth; **petioles** subterete, at least distally, (2–)3–5 mm long, sparsely to moderately hairy above and below, the hairs wavy, appressed to ascending, yellowish; **lamina** chartaceous, narrowly elliptic to oblong, oblanceolate, sometimes obovate, 60–80(–110) mm long, 22–32(–35) mm wide, the length to width ratio (2.3–)2.5–3.2 **:** 1, somewhat revolute, at least along the lower 1/2 of the margins, *apex* broadly to acutely rounded, *base* rounded to the petiole, very rarely cuneate; **lower lamina surface** moderately hairy in immature leaves, glabrate to sparsely hairy when mature, the hairs 0.2–0.9 mm long, appressed to subappressed, straight, or nearly so, more frequent in the basal 1/4 of the leaf, sparsely to moderately clavate glandular hairy, the glandular hairs amber colored, the epidermis gray in herbarium material, sometimes viscid, the stomatal apparatus often opaque, white, and conspicuous; **upper lamina surface** glabrous to sparsely pubescent with weak hairs, the epidermis weakly papillate, brown to dark gray and somewhat shiny in herbarium material, epidermal cells conspicuous with age. **Venation** brochidodromous to arcolanguid; **midrib** narrow and prominent on the lower surface, usually ≤ 1 mm wide, sparsely to moderately hairy, the hairs 0.3–0.9 mm long, slightly wavy to nearly straight, subappressed; the midrib raised proximally on the upper surface, convex, narrowing distally, becoming flush with the lamina, glabrate to sparsely pubescent, rarely moderately pubescent, the hairs ± wavy, the epidermis light yellow above and below; **lateral veins** 6–9 on each side of the midrib, diverging from midrib between 45–90°, rounding towards the apex distally, intersecondary veins inconspicuous; **3° veins** usually faint below, sometimes slightly darkened and more apparent, faintly raised or not apparent on the upper surface; **4° veins** sometimes slightly darkened and apparent below. **Laminar extrafloral nectaries** 0.2–0.6(–0.8) mm in dimension, circular to elliptic. **Male inflorescences** solitary (1–)2–3-flowered cymes in leaf axils of young stems (our description of the male inflorescence and

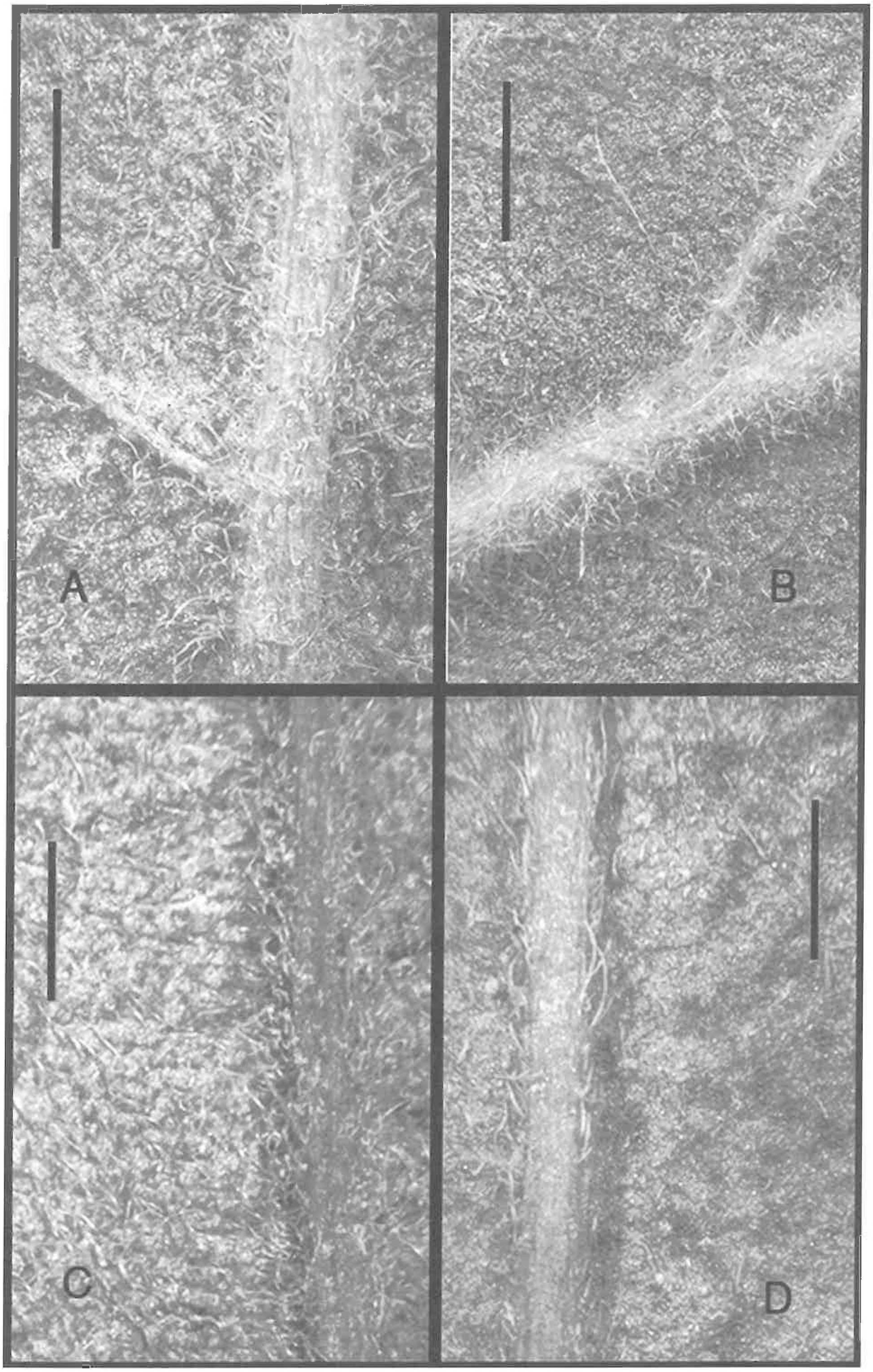

FIG. 39. Abaxial leaf vestiture, including midrib (scale = 1 mm). **A.** *D. aequoris* subsp. *chutlensis* (from the holotype). **B.** *D. aequoris* subsp. *tehuantepecensis* (from the holotype). **C.** *D. aequoris* subsp. *chutlensis* (*M.C. Provance 9930,* UCR). **D.** young leaf, *D. salicifolia* (*W. Boege 452,* FR).

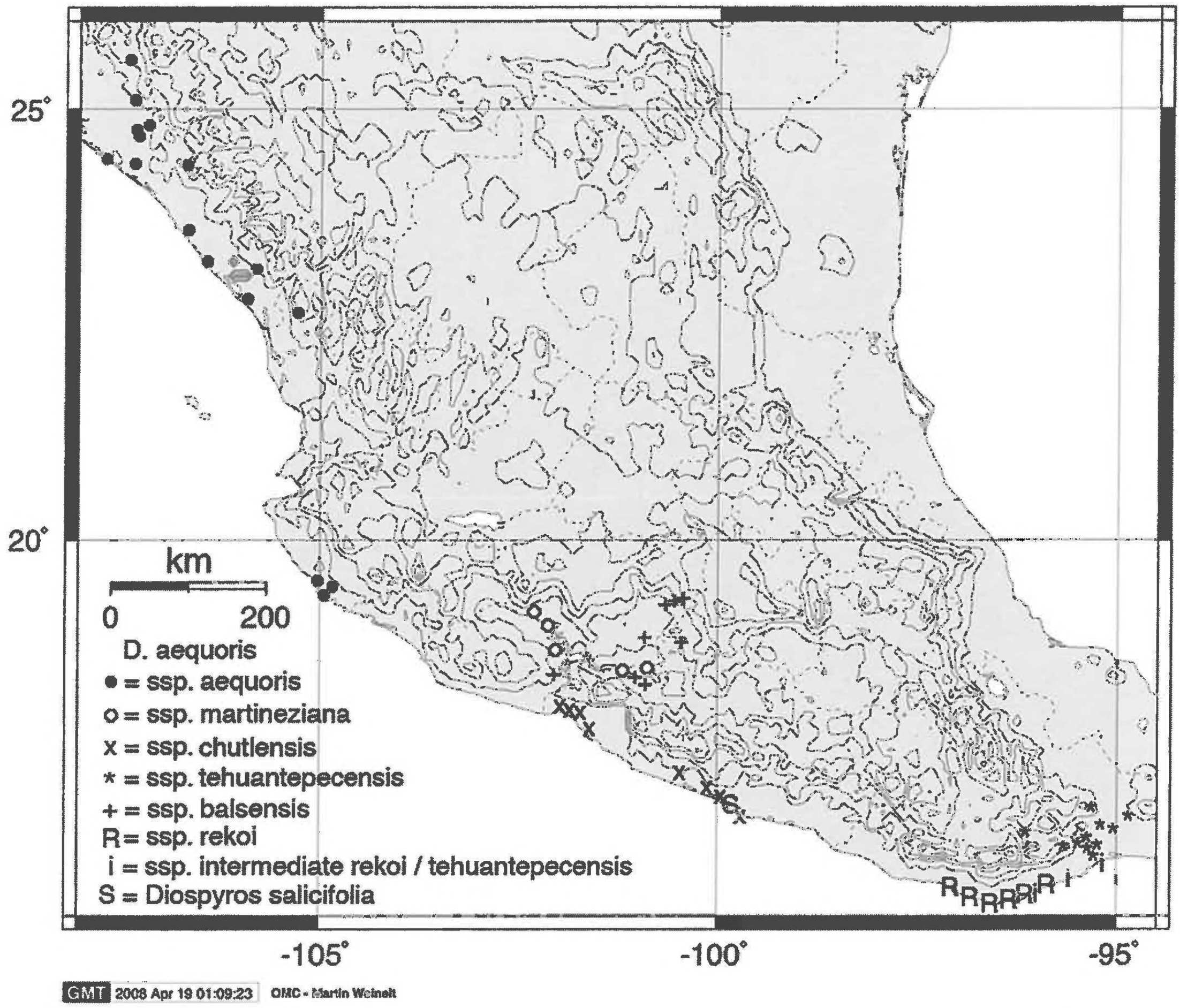

Fig. 40. Distribution of *Diospyros aequoris* Standley and *D. salicifolia* Humb. & Bonpl. ex Willd.

flowers is approximate, and lacks detail because the only male specimen we have seen is a photo of the type of *D. albens*); **peduncles** 2 mm long; **pedicels** 1–1.7 mm long. **Male flowers** 3-merous; **male flowering calyx** narrowly campanulate, *tube* 2 mm long, 2 mm wide, *lobes* valvate-reduplicate in the bud, narrowly triangular, 3–5.5 mm long, 2.2 mm wide; **male corolla tube** urceolate, 3 mm long, 2 mm wide, sericeous; **male corolla lobes** 2.5 mm long. **Stamens** of unknown number; **filaments** at least sometimes adnate to the corolla near the base; **anthers** lance-ovate, 1.5–2 mm long, opening by longitudinal slits. **Female inflorescences** solitary flowers in leaf axils of young stems; **female flowering pedicels** 3–5 mm long, vestiture similar to that of young stems. **Female flowers** 3–4-merous; **female flowering calyx** mitriform, exterior moderately hairy, the hairs very minute, subappressed, light yellow to amber, apparently borne from glandular punctae, these most obvious near the sepal margins, *tube* cupulate, 1.2–1.8 mm long, 3 mm wide, interior unknown, *lobes* valvate-reduplicate in the bud, ovate to widely ovate, winged, 6.5 mm long, 6.5 mm wide, faintly 3–6-veined; **female corolla** unknown; **ovary** unknown; **styles** (based on remnants on fruits) 3, fused into a column with a dark basal band, densely wavy-hairy, the hairs cream to amber; **stigmas** unknown. **Fruiting pedicels** 2–5 mm long, bracts 2, ± opposite, deltoid, 0.3 mm long. **Fruiting calyx** slightly accrescent, explanate to rotate, the exterior glabrate to sparsely hairy, the hairs slightly wavy to straight, subappressed; epidermis glandular punctate, glands often black, *tube* 3–4.5(–6) mm long, not bulbous at the base, interior lower 1/2 glabrous, otherwise moderately white hairy, the hairs long, fine, glossy,

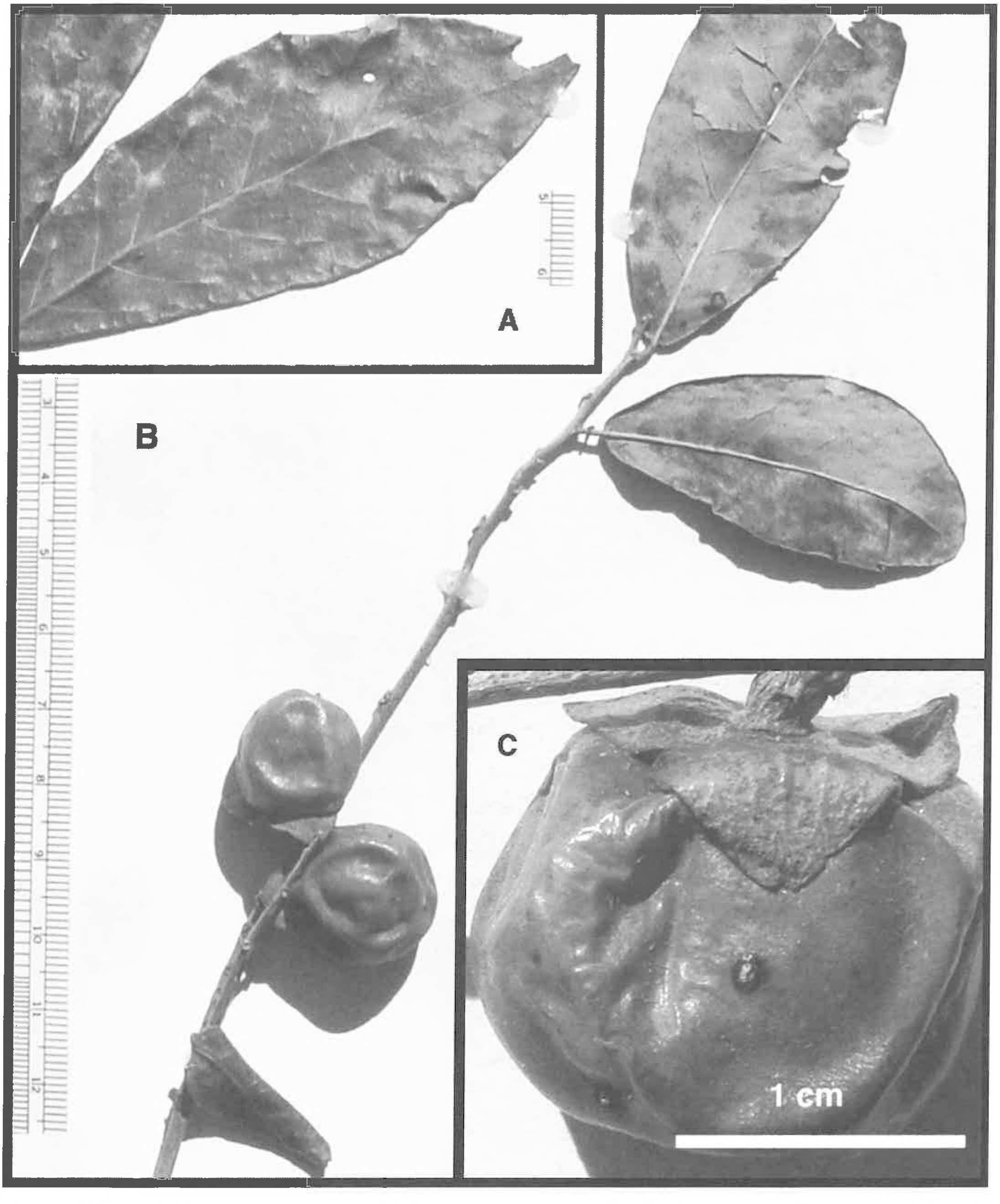

FIG. 41. *Diospyros salicifolia* from Revolcadero [Acapulco Vicinity] (*W.L. Forment 1317*, SD). **A.** Adaxial surface of leaves. **B.** Fruiting branchlet. **C.** Detail of fruit and fruiting calyx. **P.** Adaxial surface of male flowering calyx. **Q.** Male corolla tube. **R.** Male flower. **S.** Stamen.

straight and appressed, *lobes* spreading, broadly ovate to oblong-ovate, 4–6(–6.5) mm long, 8–10 mm wide, sometimes acuminate, often reflexed along the margins, with a wide interior intramarginal band of hairs, the hairs dense, minute, curly, the median similar to the upper 1/2 of the fruiting calyx tube. **Fruit** a ± globose berry, 2–2.5 cm in diameter, with three pairs of locules; **flesh** probably gelatinous when fresh, vitreous, red

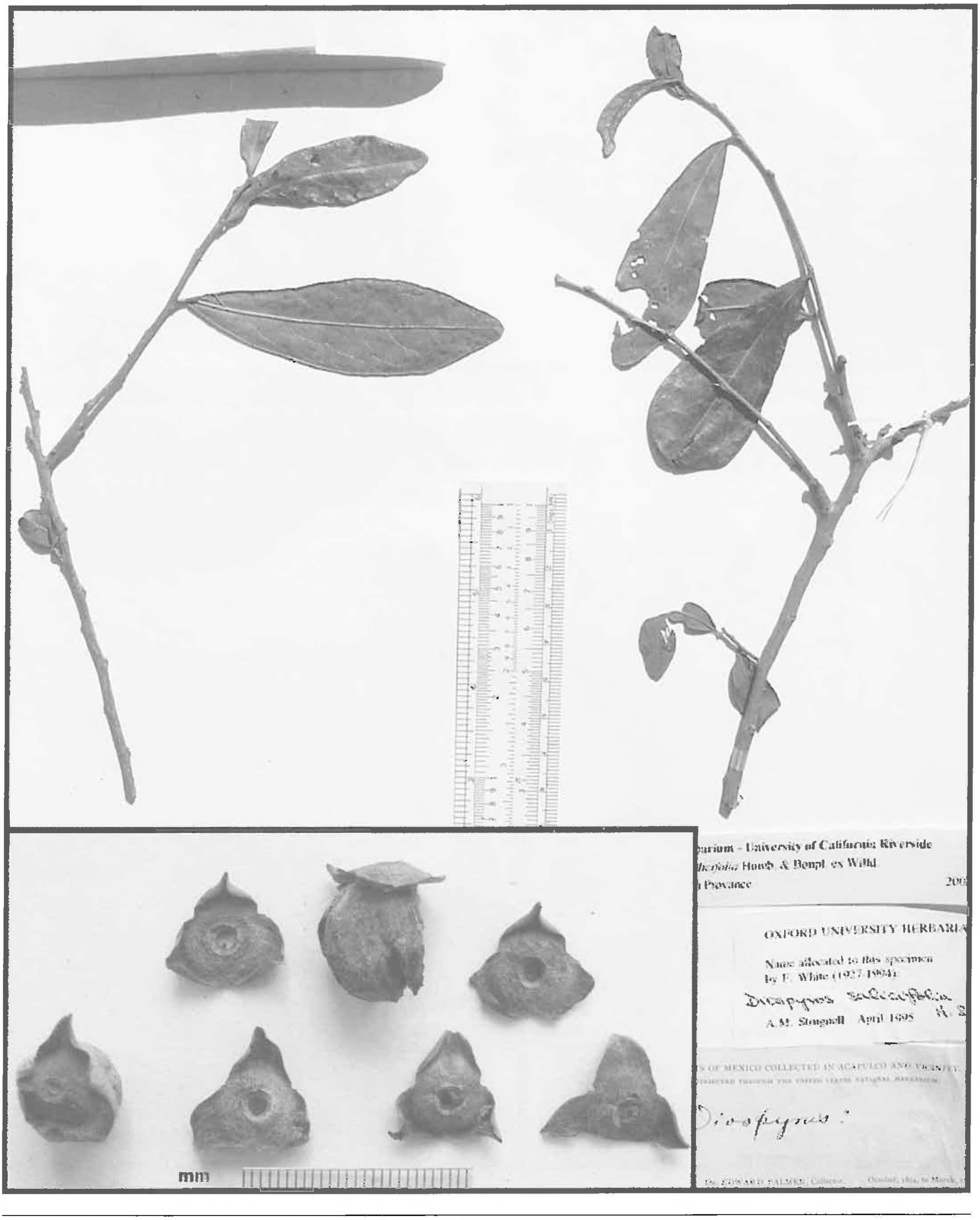

Fig. 42. Fruiting branchlet of *Diospyros salicifolia* (*E. Palmer 372*, MO), with detail of fruit and fruiting calyx.

and translucent upon drying; **epidermis** smooth to orange-peel textured, sparsely to moderately hairy near apex and base of the fruit, otherwise glabrous or scantily appressed hairy, the epidermis yellow to dark yellow when mature, often pruinose. **Seeds** 5–6, wedge-shaped (resembling an orange segment with rounded edges), 15 mm long, 8 mm radial depth, 6 mm wide, reddish-brown, texture granular-foveolate.

Diospyros salicifolia is endemic to dry tropical forest and littoral scrub between 1 and 100 m, in the vi-

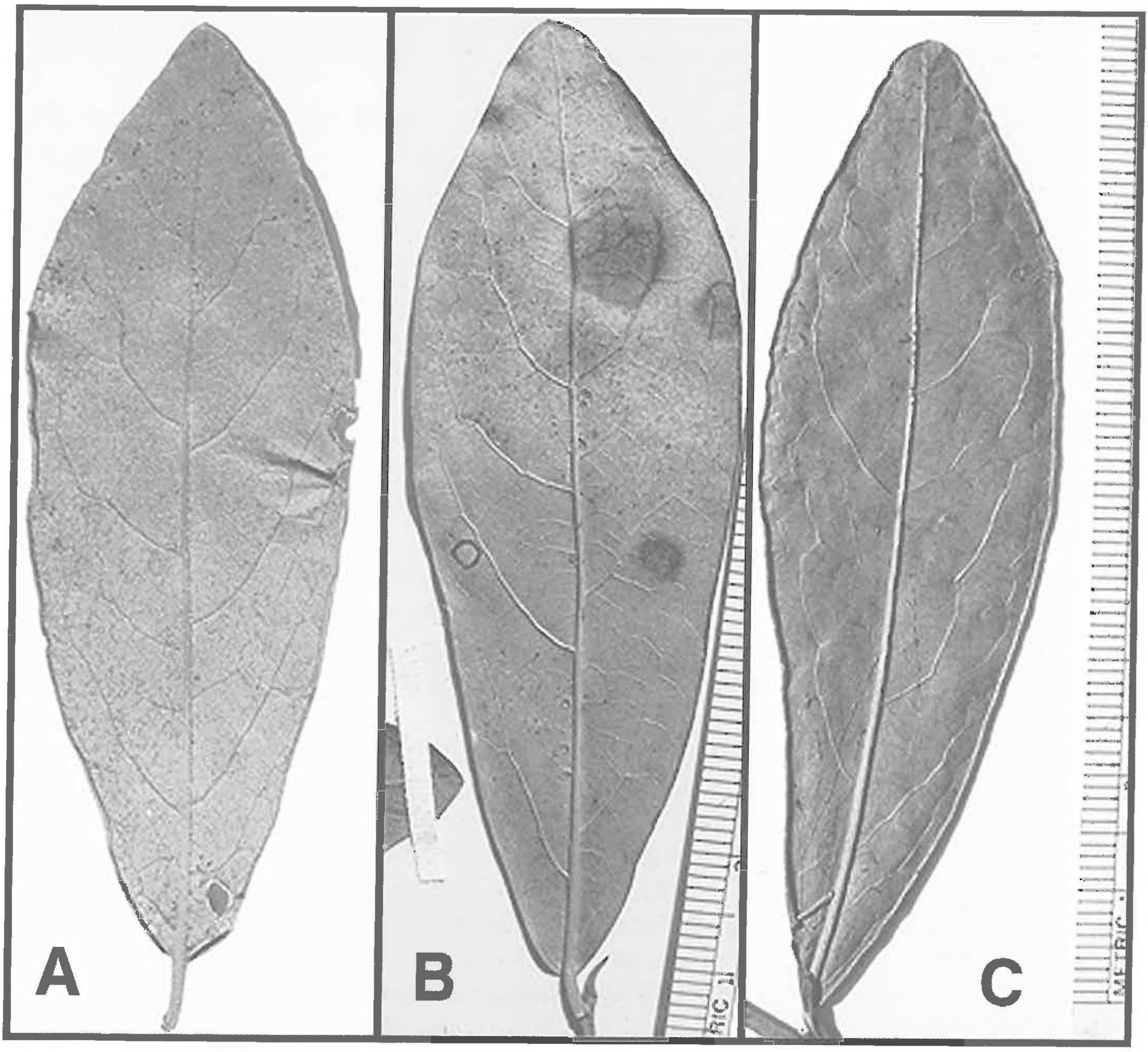

FIG. 43. Detail of abaxial surface of leaves of *Diospyros salicifolia*. **A.** Young leaf from Copacabana [near El Marques, Acapulco Vicinity], Guerrero (*W. Boege 452*, FR). **B.** From Puerto Marqués, Guerrero (*W.L. Forment 1338*, XAL). **C.** From Acapulco and vicinity (*E. Palmer 372*, MO).

cinity of Acapulco and Isla Roqueta (Isla Grifo) at the mouth of Acapulco Bay, Guerrero (Fig. 40). Protected forests exist in the vicinity of Acapulco, but it is unknown if the species occurs in these areas. Because of its restricted range, apparent association with littoral scrub, and proximity of a rapidly developing tourism center, the species should be considered threatened. Local names associated with this species include "tamalototzin" and "sapotillo." The fruiting calyx of this species is quite small and similar to *D. aequoris* subsp. *chutlensis*. However, the leaves of *D. salicifolia* are longer and have a greater lamina shape ratio. The foliage of collections of *D. acapulcensis* subsp. *veraecrucis* from coastal regions of Chiapas sometimes resembles *D. salicifolia*, but fruiting calyces have the longer tube typical of subsp. *veraecrucis*. Material from this region should be evaluated more thoroughly when more collections are available.

Representative specimens. **MEXICO. GUERRERO. Mpio. Acapulco de Juarez:** Isla Roqueta, *I.K. Langman 3305* (NA); portum Acapulco, *Haenke 31942* (W photo); Copacabana [location near El Marques, 16°46'12"N, 99°47'24"W, 1–3 m, (The label incorrectly places Copacabana in "Puebla/Tlaxcala." The date is suspect also.), 15 Jul 1966, *W. Boege 452* (FR); Viveros El Huayacán, La Poza, 22 May 1979, *W.L. Forment 790* (XAL); 2 km W de Puerto Marqués, 19 Jan 1981, *W.L. Forment 1388* (CAS, JBSD, MO); Puerto Marqués, 28 Jan 1981, *W.L. Forment 1338* (XAL); Acapulco and vicinity, Oct 1894–Mar 1895, *E. Palmer 372* (MO); Revolcadero, 27 Jan 1981, *W.L. Forment 1317* (SD, XAL).

4. Diospyros yucatanensis Lundell. Publ. Carnegie Inst. of Wash. 478:217. 1937. TYPE: GUATEMALA. PETEN. San Andres [as on label], "collected on the steep north bank of Lake Petén near San Andres" [protologue], 4 May 1933, *Lundell 3237* (HOLOTYPE: MICH; ISOTYPE: F-685309, as image!, LL).

Trees or shrubs, 2–15(–28) m tall, facultatively deciduous, dioecious; **trunk** often relatively tall and slender, otherwise unknown; **wood** unknown; **mature stems** terete, half-netted to finely reticulated, glabrous, epidermis dark reddish-brown to grayish-brown, sometimes lenticellate, sometimes black gland dotted; **2nd year stems** subterete to terete, nearly smooth, minutely ridged or sulcate, glabrous to densely hairy, the hairs when present often pale and desiccated; **1st year stems** angular to subterete, sometimes rugulose, moderately to densely hairy, the hairs short, wavy to curly, sometimes longer and nearly straight, orangish to reddish-brown (the hairs throughout the plant are mostly simple glandular hairs, likely translucent in life, and the color of hairs in herbarium specimens is due to darkening of a fluid in the lumen), clavate glandular hairs sometimes present, deciduous, leaving the epidermis viscid, sometimes scintillant, sometimes pruinose, reddish-brown. **Leaves** alternate, simple, entire; **petioles** (2–)3.5–8(–8.5) mm long, sometimes winged, often only distally, glabrous to densely hairy, epidermis usually rugose, often viscid, sometimes glaucous, sometimes pruinose, sometimes scintillant, golden to very dark brown, barely canaliculate to convex above; **lamina** chartaceous, (52–)59–106(–123) mm long, 19–41(–48) mm wide, length to width ratio (1.8–)2.1–3.5(–4) **:** 1, lanceolate or ovate, sometimes oblanceolate, obovate, or elliptic, at 3/4 length mostly 12–30(–35) mm wide, *base* acute and short attenuate to broadly rounded, usually somewhat decurrent on the petiole, *margins* flat to slightly revolute, *apex* acuminate to acute, sometimes rounded; **lower lamina surface** glabrate to densely hairy, curly to slightly curved, sometimes straight, cream to tawny to bright orange-red, hair bases usually swollen and ± papillose, epidermis grayish, sometimes viscid, the stomatal apparatus usually opaque and conspicuous; **upper lamina surface** glabrous to moderately hairy, the hairs wavy, upright, epidermis sometimes shiny, sometimes crystal-papillose. **Venation** brochidodromous to arcolanguid, the epidermis yellowish to reddish-brown and sometimes viscid below; **midrib** prominent below, glabrous to densely hairy, the hairs short, curly, with some longer, straight, subappressed, bright reddish-brown hairs; **lateral veins** 5–8 on each side of the midrib, their courses mostly arching, thin but ± prominent below, often with long, straight, bright reddish-brown hairs, fine and barely raised to flush above, impressed along the lamina-vein seam; **3° veins** subprominent below, though usually somewhat obscured by the vestiture, usually obscure above, sometimes slightly impressed; **4°–5° veins** obscure. **Laminar extrafloral nectaries** usually on basal half of leaf, often near midrib, sometimes on intersecondary veins, mostly elliptic, 0.3–1 mm long, concave. **Male inflorescences** 1–5-flowered cymes in leaf axils on young stems, densely hairy, the hairs minute, curly to wavy, reddish; epidermis viscid and dark brown; **peduncles** 2–6 mm long; **pedicels** 1–3 mm long, bracts ovate or deltoid to linear lanceolate, 1–3 mm long. **Male flowers** 3–4-merous; **male flowering calyx** narrowly campanulate, exterior moderately to densely hairy, the hairs straight to curly, golden to reddish, the epidermis reddish-brown, *tube* 3–5.5 mm long, 3.5–5.5 mm wide, interior entirely glabrous, or glabrous in the lower half and densely hairy above, the hairs straight, appressed, *lobes* valvate-reduplicate in the bud, oblong-ovate to lance-ovate or triangular, 2–4 mm long, 2.8–3.5 mm wide, acute to subacute, sometimes barely acuminate, interior intramarginal band narrow, moderately to densely hairy, the hairs minute and curly, the median hairs moderate to dense, the hairs straight or nearly so, appressed to subappressed; **male corolla** white, yellowish or pinkish; **male corolla tube** cylindrical, narrowing distally, 6–10 mm long, 3–4 mm wide, exterior with 3 small shield-shaped glabrous regions at base, or with a narrow glabrous basal band, sometimes with minute wavy hairs just distal to glabrous areas, otherwise tawny to reddish sericeous with a dense undercoat of minute curly hairs; **male corolla lobes** oblong-ovate, 3–5 mm long, 1–2.3 mm wide, exterior densely hairy, the hairs curly to straight, subappressed to ascending, reddish-gold to brownish, the epidermis reddish to dark reddish-brown. **Stamens** 10–14; **filaments** adnate to the corolla at or near the base, in two well-defined tiers, or with a few stamens inserted on the receptacle, sometimes a few geminate, (1.5–)2–3.5 mm long; **anthers** lanceolate to ovate or oblong-ovate, 2.3–4.5 mm long, lower anthers usually shorter, apex sometimes rostrate or cuspidate, sometimes thickened or granular near the apex; **pistillode**

minute, hairs dense, wavy or straight. **Female inflorescence** solitary flowers in leaf axils of young stems, the vestiture similar to male inflorescences; **female flowering pedicels** with hairs and epidermis similar to male inflorescences. **Female flowers** 3–4(–5)-merous; **female calyx** mitriform, sometimes narrowly winged, *tube* 2.5–3.3 mm long, 4–5 mm wide, *lobes* valvate-reduplicate in the bud, bluntly acute to slightly rounded, 3.3–6 mm long, 3.5–5.5 mm wide; **corolla tube** urceolate, narrowing distally, 3–5 mm long, 2.5–3 mm wide, exterior reddish sericeous except for some glabrous parts near the base; **corolla lobes** lance-ovate to ovate, 3.5–4.5 mm long, 1.5–2.5 mm wide; **ovary** ovoid, sericeous, the hairs reddish and fluid-filled; **styles** 3, columnar to spreading; **stigmas** bifid; **staminodes** sometimes present. **Fruiting pedicels** 2–14(–16) mm long, broadening distally, glabrate to densely hairy, the hairs short, wavy, subappressed to appressed, often pale and desiccated on mature fruit, epidermis reddish to brownish, bracts not seen. **Fruiting calyx** rotate to explanate, exterior hairs similar to fruiting pedicels, *tube* 3–6(–7.5) mm long, interior sparsely to densely hairy, the hairs very short, fine, straight and appressed, but glabrous in the basal 1/8–1/3, *lobes* accrescent, broadly rounded to oblong, 3–10(–12) mm long, (7–)9–14(–15) mm wide, spreading to reflexed, the margin sometimes conspicuously undulate, tip rounded, tapered or barely acuminate, sometimes appearing narrowed to a point due to folding of the distal margin, intramarginal band very wide, sparsely to moderately hairy, the hairs minute, curly, erect to ascending, amber; the epidermis puncticulate viscid; median sparsely to moderately hairy, the hairs similar to those of inner calyx tube, present only near the base of lobe. **Fruit** a globose to depressed-globose berry, 1.5–2.5 cm in diameter, sometimes umbilicate, often partly dehiscent, consistently with three pairs of locules, immature fruit sparsely reddish-brown hairy, mature fruit glabrate except near apex where hairs may be dense, and at base where a ring of subappressed, fine, straight hairs is sometimes present (the ring sometimes adhering to the base of the fruiting calyx tube); **flesh** gelatinous; drying vitreous, reddish and translucent; **epidermis** texture ± orange-peel like, often pruinose, scintillant, sometimes glaucous, golden brown to reddish-brown, sometimes yellow. **Seeds** shaped like orange segments, texture rugulose-foveolate, 11–14 mm long, 6–7 mm radial depth, 4–5 mm wide.

The range of this species includes the Yucatan Peninsula, the highlands of northern Chiapas, Tabasco, southeast Veracruz, and northeast Guatemala (Fig. 49). The southern limit of its range seems to be near Lake Izabal, Guatemala. Collections from "El Rancho" on the southern slopes of the Sierra de las Minas in Guatemala are difficult to place, and are thought to represent hybrids between the nominate subspecies of *D. yucatanensis* and *Diospyros acapulcensis* subsp. *nicaraguensis*. The species seems to be associated with thin rocky soils throughout its range. Lundell (1937) described two species in the *salicifolia* complex for the Yucatan Peninsula: *Diospyros yucatanensis* and *D. spectabilis*. We recognize only one species, *Diospyros yucatanensis*, separated from other members of the complex based on differences in leaf shape and several inflorescence size and shape parameters. *Diospyros yucatanensis*, even when sterile, is easily separable from *D. aequoris* and *D. acapulcensis*. Its leaves are frequently lanceolate to lance-ovate, a feature not seen elsewhere. On the abaxial surface of the leaf the hair bases are usually swollen and slightly viscid. This gives a characteristic papillose appearance to older leaves that have lost their hair shafts. Characteristics of some floral features also seem be of taxonomic significance, such as the longer corolla tube, differences in the distribution of the external vestiture on the corolla tube, and a trend toward fourteen stamens rather than twelve. However, it would be desirable to evaluate the constancy of these characters further when there is access to larger samples of flowers. We have reduced *D. spectabilis* to subspecific status under *D. yucatanensis* because it shares the aforementioned leaf characters and trends in floral morphology, and because intermediates between the taxa are common. Still, *D. y.* subsp. *spectabilis* warrants subspecific recognition because throughout most of its range it can be differentiated from the nominate subspecies by its longer pedicels, longer and distinctively shaped fruiting sepals, and generally narrower leaves. The ranges of the two taxa are more or less parapatric.

KEY TO THE SUBSPECIES OF *DIOSPYROS YUCATANENSIS* IN MESOAMERICA

1. Fruiting pedicels 2–6(–8) mm long; calyx lobes 3–6(–8) mm long; lamina wide, especially in the upper-half, usually 19–30 mm wide at 3/4 length; usually < 350 m, but occasionally to 1400 m _____ subsp. **yucatanensis**

1. Fruiting pedicels mostly 6–16 mm long; calyx lobes 4.5–10(–12) mm long; lamina narrow, especially in the upper-half, usually 12–23 mm wide 3/4 length; < 250 m _____ subsp. **spectabilis**

4a. Diospyros yucatanensis Lundell subsp. **spectabilis** (Lundell) M.C. Provance, I. García & A.C. Sanders, comb. et stat. nov. (**Figs. 44, 45, 47p–s, 48a–b**). Basionym: *Diospyros spectabilis* Lundell, Publ. Carnegie Inst. Wash 478:218. 1937. Type: MEXICO. Campeche: Tuxpeña, "secondary swamp forest at Tuxpeña" [protologue], [18°27'N, 90°5'W, 213 m], 11 Oct 1931, *C.L. Lundell 807* (holotype: MICH; isotypes: K!, LL, MO, as digital image!, WIS!).

Trees or shrubs, 2–10(–14) m tall; **trunk** up to 13 cm in diameter; **mature stems** glabrous, rarely with remnant hairs in the 2nd year, the young stems glabrate to sparsely villosulous, some hairs subappressed, the epidermis viscid, pruinose, scintillant. **Petioles** (2–)3.5–8(–8.5) mm long, sometimes with a thin wing, rugose, golden to dark reddish-brown, sometimes pruinose and scintillant, viscid, glabrous to sparsely pubescent or wavy-hairy below, the hairs appressed to subappressed, ascending to subappressed villosulous above. **Lamina** lanceolate or ovate to elliptic, sometimes oblanceolate or obovate, (52–)59–96(–123) mm long, 19–38(–48) mm wide, length to width ratio (1.8–)2.1–3.5(–4) **:** 1, lamina at 0.75 length 12–24(–35) mm wide, *base* acute, sometimes obtuse, short attenuate and abruptly decurrent on the petiole, *margins* slightly revolute, *apex* acuminate or acute, sometimes rounded; **lower lamina surface** glabrate to tomentulose, the cream, tawny, or reddish hairs readily deciduous, the hair bases swollen, giving a dense papillose appearance to the reddish-brown to gray epidermis, the stomatal apparatus dense, usually opaque and conspicuous; **upper lamina surface** glabrous to sparsely villosulous, epidermis viscid and shiny. **Venation** brochidodromous to arcolanguid; **midrib** below glabrous to densely reddish-brown hairy; **lateral veins** finely raised below, usually impressed along the lamina-vein seam above; **3° veins** barely raised below, slightly impressed above. **Male inflorescences** 1–3-flowered cymes, tomentulose and sparsely subappressed pubescent; **peduncles** 4–6 mm long; **pedicels** 2–2.5 mm long, bracts ovate to deltoid, 1–1.3 mm long, ± concave, readily deciduous. **Male flowering calyx** moderately to densely reddish-gold puberulent outside, the hairs minute, ± straight, not overlapping, *tube* 3–4 mm long, 3.5–4 mm wide, glabrous inside, or with scattered hairs below the sinuses, *lobes* oblong-ovate to lance-ovate, 2–4 mm long, 3.5 mm wide, acute or barely acuminate, minutely sericeous inside with a narrow intramarginal band; **male corolla tube** 6–7.5 mm long, 3.2 mm wide, sericeous and either glabrous for 0.5–0.8 mm basally, or with 3 minute shield-shaped glabrous basal regions; **male corolla lobes** lanceolate to lance-ovate, 3.5–5 mm long, 1–1.8 mm wide, the hairs reddish-gold. **Stamens** 10–14; **filaments** adnate to the corolla ± basally in two well-defined tiers, 2–2.5 mm long, red; **anthers** lanceolate to lance-ovate, 2.3–3 mm long. **Female inflorescences** 7–9 mm long, bracts unknown. **Female flowering calyx** narrowly winged, densely reddish subappressed wavy-hairy outside, sometimes with some straight ascending hairs, vestiture inside unknown *tube* 3.3 mm long, 4 mm wide, *lobes* acute, 3.3 mm long, 3.5 mm wide; **corolla tube** 4–5 mm long, ± 3 mm wide, reddish sericeous outside, otherwise unknown; **corolla lobes** lance-ovate, 3.5–4.5 mm long, 1.5 mm wide. **Pistil** unknown except **style remnants on immature fruit** 3 in number. **Fruiting pedicels** (3–)5–14(–16) mm long, glabrate to moderately hairy, viscid. **Fruiting calyx tube** 3–6(–7.5) mm long, upper 2/3 sparsely to moderately hairy inside, lower 1/3 glabrous, *lobes* rapidly and markedly accrescent, broadly rounded to oblong, (3.5)4–10(–12) mm long, (8–)9–14(–15) mm wide, rounded to barely acuminate to a blunt point, spreading to reflexed, margins reflexed at the sinus and along the distal margin conferring the appearance of a narrowly acute to acuminate point, sparsely to moderately hairy inside with a wide intramarginal band. **Fruit** globose to depressed-globose, sometimes umbilicate, immature fruit sparsely reddish-brown hairy, mature fruit glabrous except moderately hairy at the apex.

This northern subspecies grows on thin, rocky, calcareous soils in deciduous and subdeciduous forests, and secondary growth derived from these vegetation types. It occurs below 250 m elevation throughout the Yucatan Peninsula, Mexico, (Fig. 49), in the states of Campeche, Quintana Roo, and Yucatan. It also has a limited range in northeast Guatemala and Belize. This taxon is separable from the nominate subspecies by its longer fruiting pedicels, longer and slightly wider fruiting sepals, and slightly shorter and narrower lamina. There seems to be a difference in lamina pubescence, but it is subtle, and of limited use since lamina

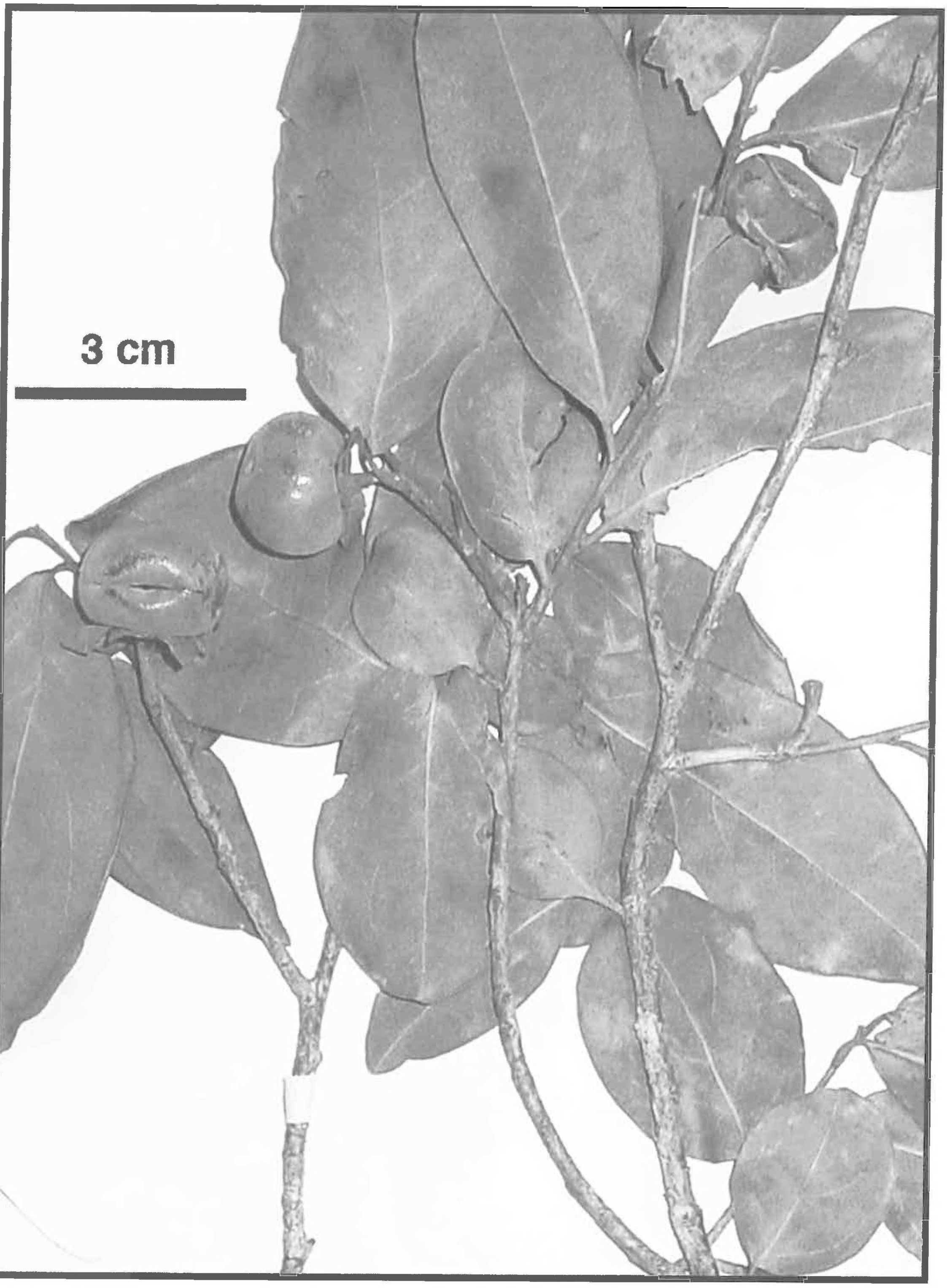

FIG. 44. Isotype of *D. spectabilis* Lundell (*D. yucatanensis* Lundell subsp. *spectabilis* (Lundell) M.C. Provance, I. García & A.C. Sanders, comb. nov.), from Tuxpeña, Campeche, Mexico, *C.L. Lundell 807* (WIS).

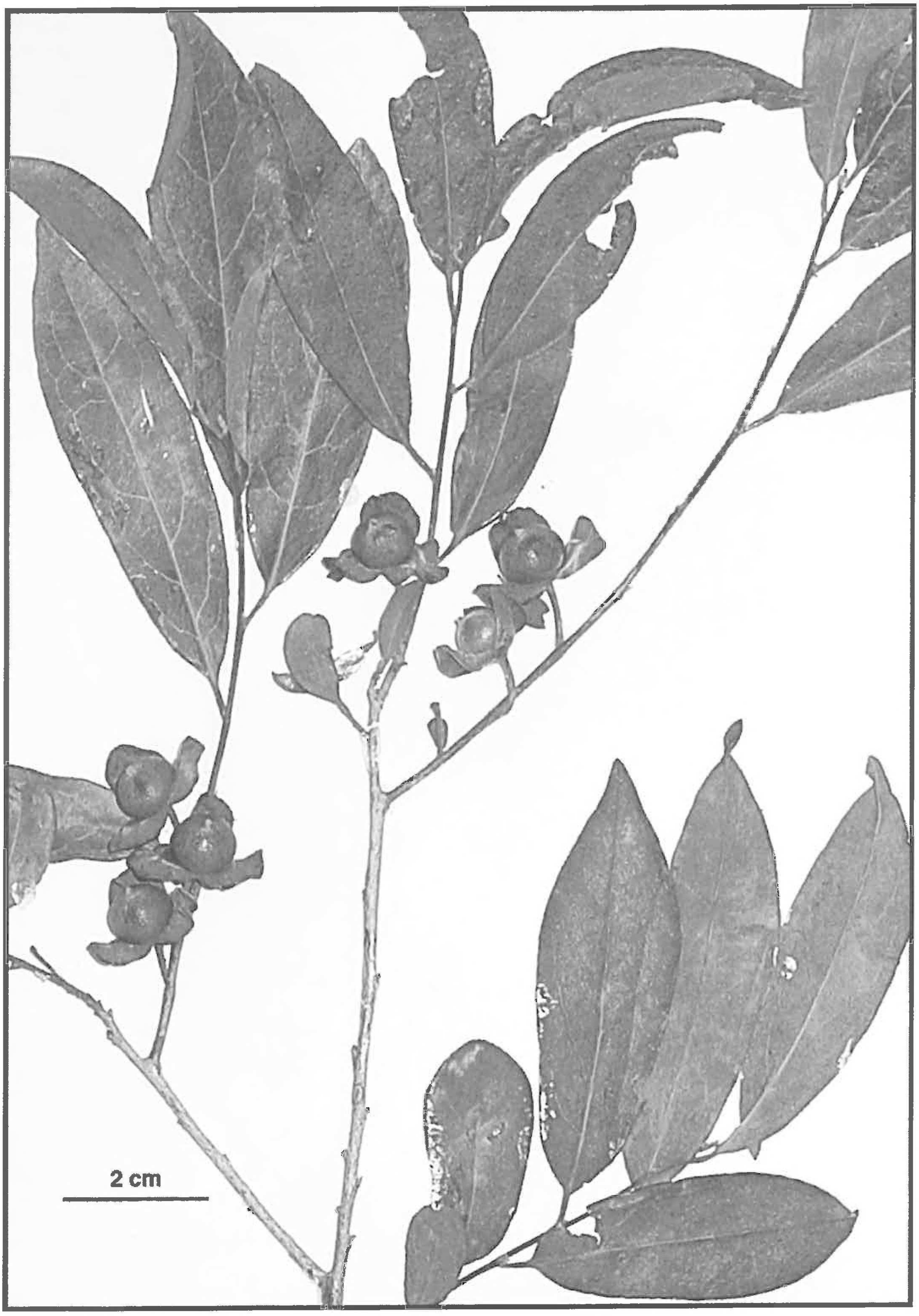

Fig. 45. *Diospyros yucatanensis* subsp. *spectabilis* from Maxcanú, Yucatan, Mexico, *C. Chan 6864* (CIQR).

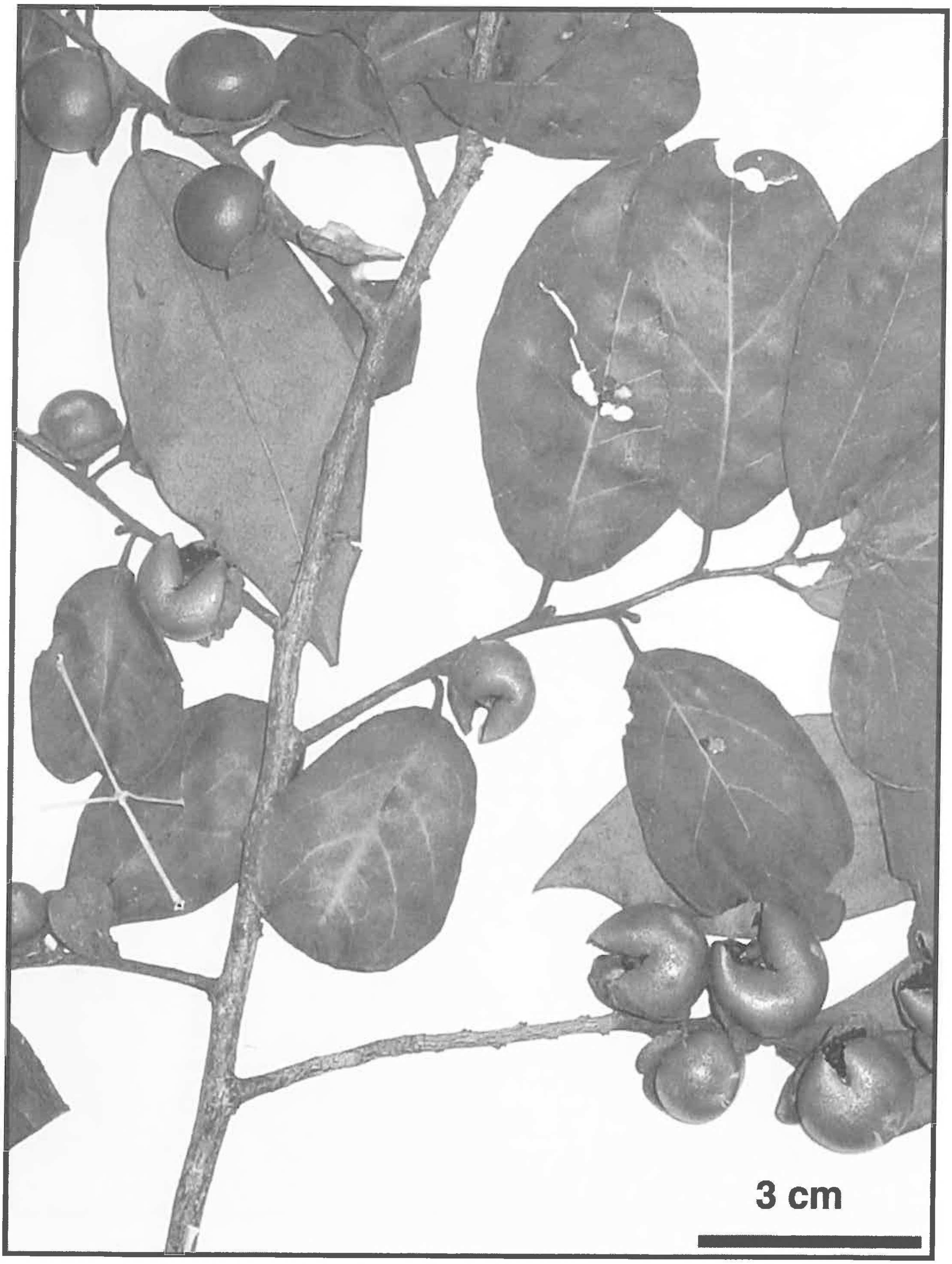

FIG. 46. Diospyros yucatanensis subsp. yucatanensis from Lago Peten Itza, Guatemala (B. Wallnöfer & F.M. Tut-Tesucun 5941, MO).

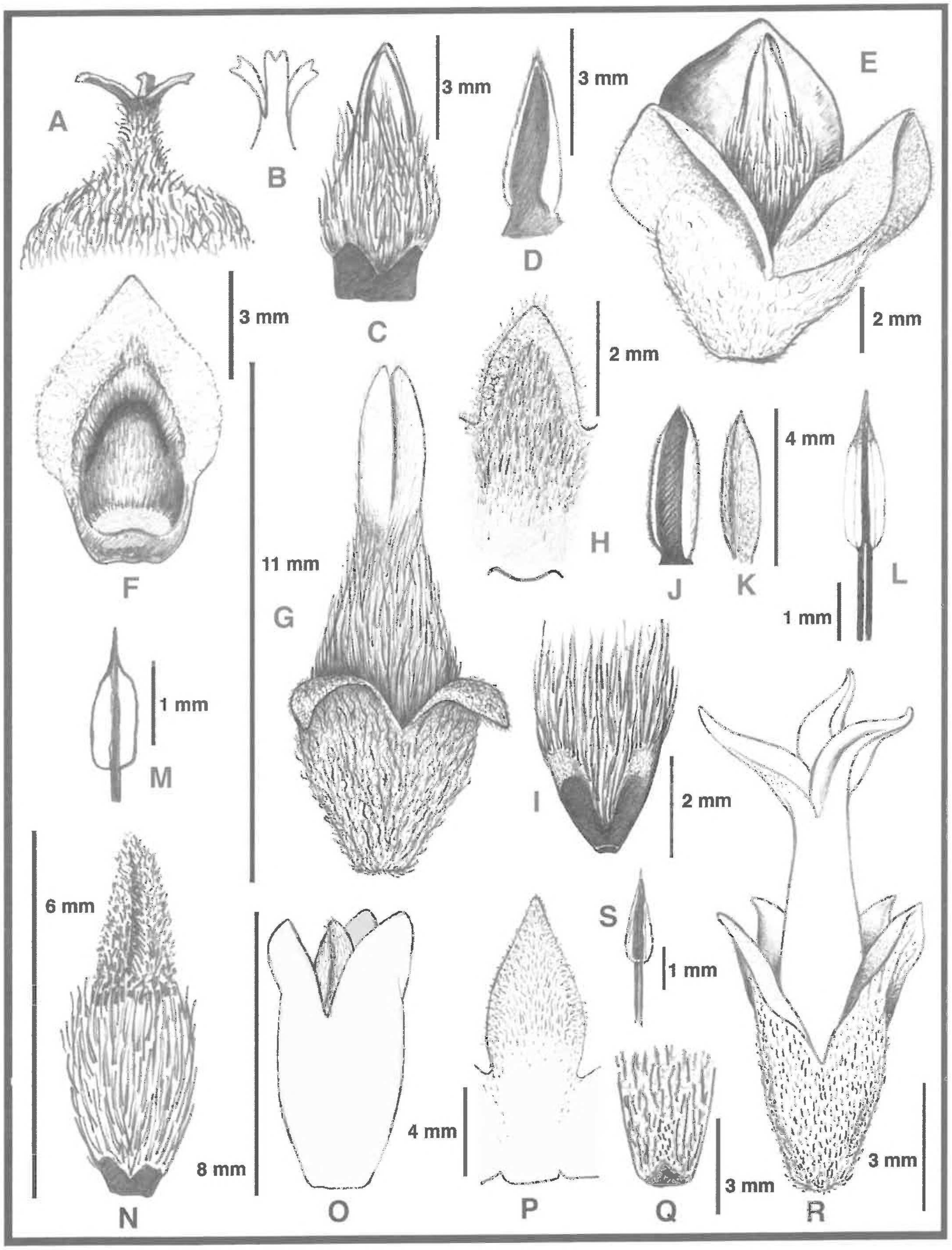

FIG. 47. *Diospyros yucatanensis* Lundell. **A–F.** subsp. *yucatanensis* from Tikal N.P. (*C.L. Lundell 16257,* IJ). **A.** Pistil. **B.** Diagram of styles and stigmas. **C.** Female corolla. **D.** Female corolla lobe. **E.** Female flower. **F.** Adaxial surface of female flowering calyx. **G–L.** subsp. *yucatanensis* from San Isidro, Tabasco, Mexico (*E. Matuda 3378,* NA). **G.** Male flower. **H.** Adaxial surface of male flowering calyx. **I.** Male corolla tube. **J.** Male corolla lobe (adaxial side). **K.** Male corolla lobe (abaxial side). **L.** Stamen. **M–O.** subsp. *yucatanensis* from Río Dulce, Izabal, Guatemala (*Steyermark 39427,* F). **M.** Stamen. **N.** Male corolla. **O.** Male flower. **P–S.** subsp. *spectabilis* from Quintana Roo, Mexico (*C. Gallardo et al. 2220,* MO). **P.** Adaxial surface of male flowering calyx. **Q.** Male corolla tube. **R.** Male flower. **S.** Stamen.

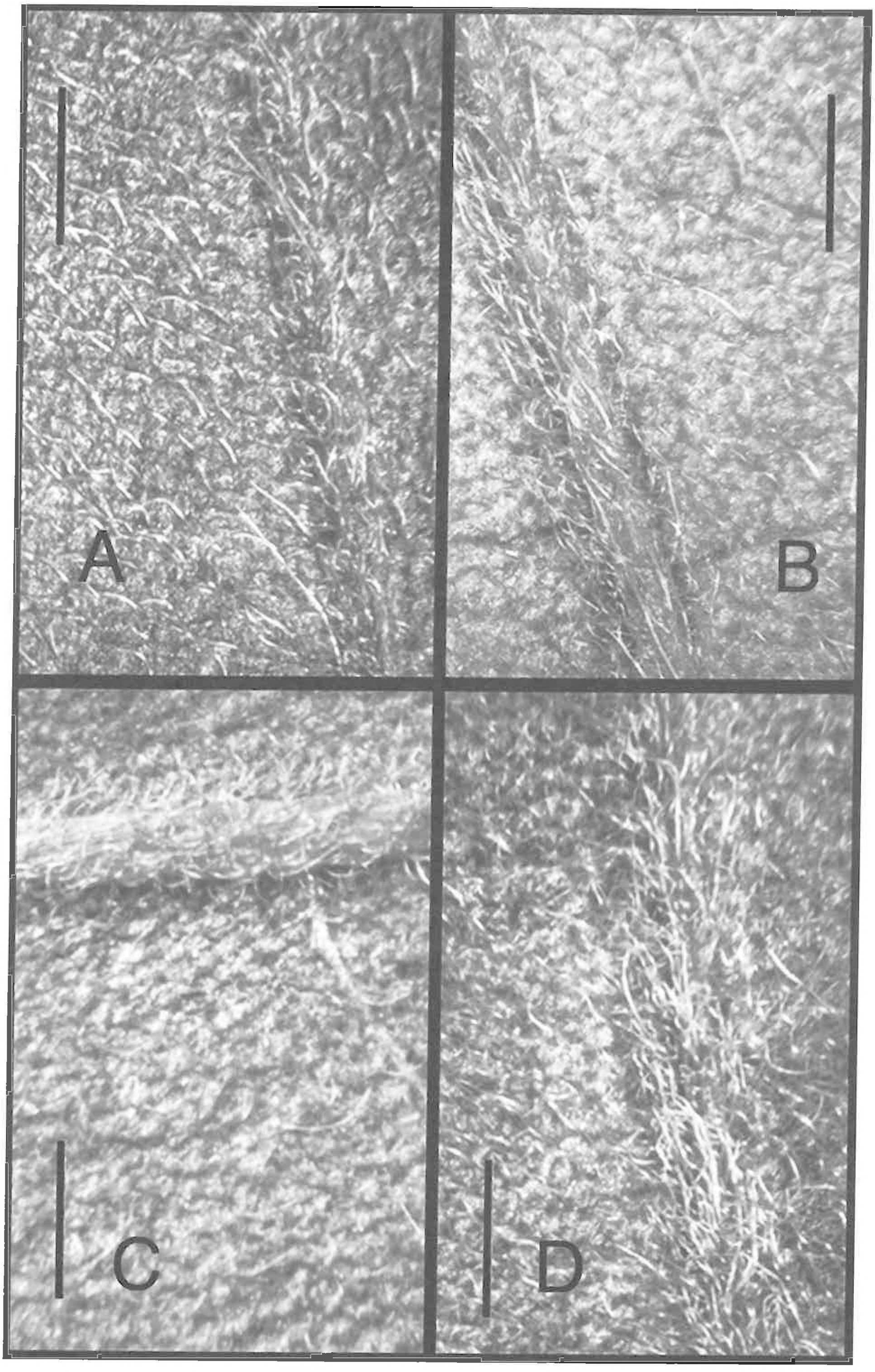

FIG. 48. Abaxial leaf vestiture, including midrib, of *D. yucatanensis* (scale = 1 mm). **A.** subsp. *spectabilis* (*J.D. Dwyer 12747*). **B.** subsp. *spectabilis* (*Schultz 1530,* UCR). **C.** subsp. *yucatanensis* (*Cabrera 14830,* MO). **D.** subsp. *yucatanensis* (*C.L. Lundell 6807,* ARIZ).

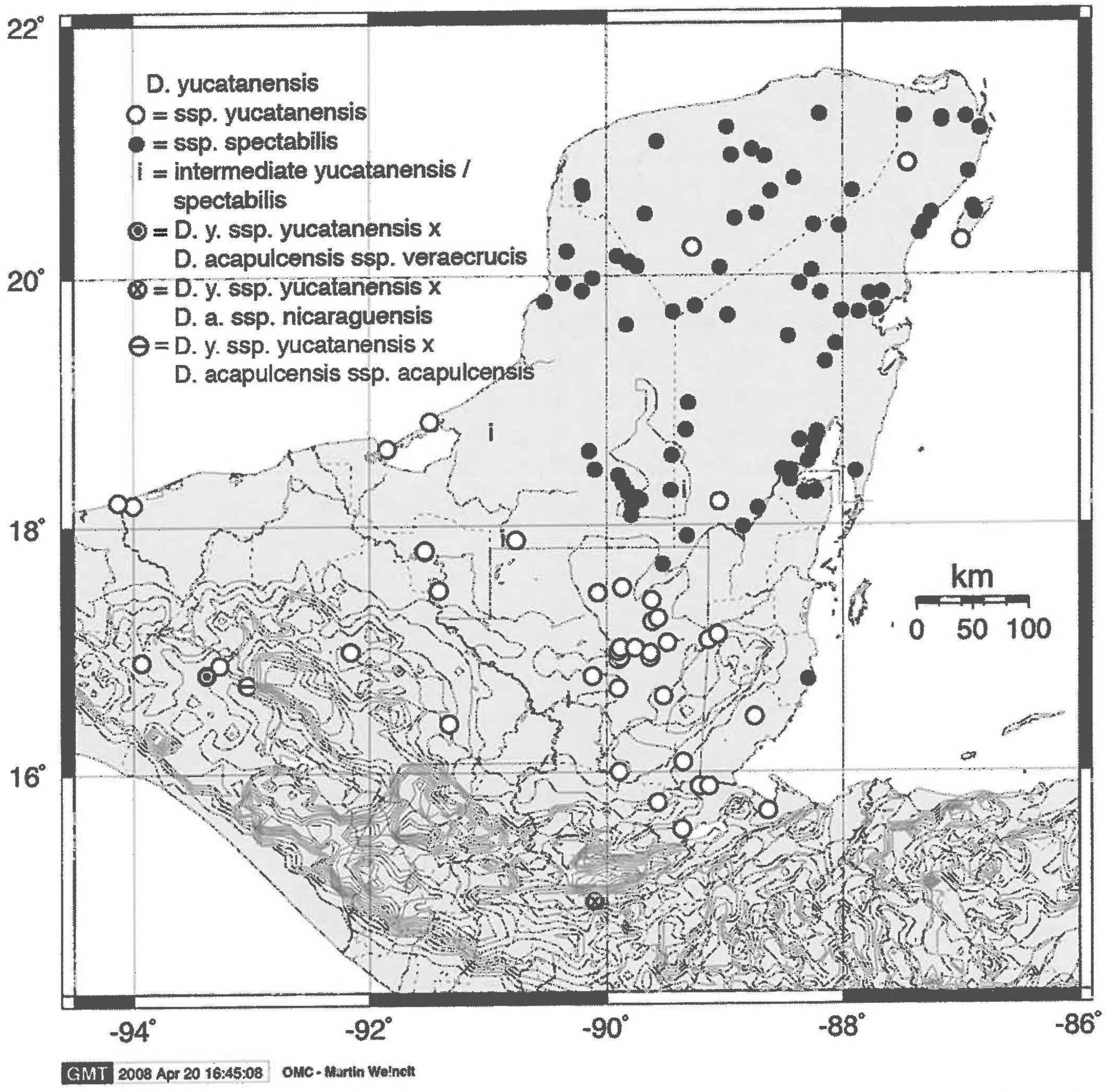

Fig. 49. Distribution of *Diospyros yucatanensis*.

vestiture tends to be deciduous in both, though the vestiture of this taxon seems to be even less persistent than in the nominate subspecies.

Representative specimens. **BELIZE. Corozal:** 5 km NW of Chan Chen, 10 m, 16 Nov 1989, *M.J. Balick 2189* (BRH). **Orange Walk:** from mi 50, Northern Hwy. to new river toll bridge, 7 Jun 1974, *J.D. Dwyer 12747* (UMO, WIS, IJ, BRH, MO). **Stan Creek:** All Pines, 0 m, 12 May 1976, *G.R. Proctor 36205, 36207* (IJ). **GUATEMALA. Peten:** P.N. Río Azul, 0.5 km antes de llegar al Cedro Bosque, 20 Feb 2000, *M. Peña-Chocarro et al. 859* (BM); Dos Lagunas, 9 km E of village, 25 Nov 1960, *E. Contreras 1651* (IJ, F). **MEXICO. Campeche. Mpio. Calakmul:** central chiclera Buenfil (Calakmul), 24 Feb 1994, *J.M. Kantún 305* (UCAM). **Mpio. Campeche:** 1 km S de Samulá, 40 m, 1 May 2003, *C. Gutiérrez B. 7761* (UCAM). **Mpio. Escárcega:** desv. carr. Escárcega a Villahermosa, rumbo a Pital, 5 m, 29 Jan 1986, *C. Chan 6102* (CIQR). **Mpio. Hecelchacán:** carr. 5 km E de Cumpich con dirección a Bolonchén de Rejón, 3 Feb 2002, *G.G. Cabrera M. 12* (UCAM). **Mpio. Hopelchén:** Rancho El Carmen, near Xpanzil, 33–35 km S of Xmaben, 200 m, 13 Mar 1990, *A.C. Sanders et al. 9752* (SD, UCR). **Mpio. Tenaba:** entre San Pedro y Santa Rita, 28 Oct 1997, *P. Zamora C. & H. Uc C. 5890* (UCAM). **Quintana Roo. Mpio. Benito Juarez:** Cancun, 25 Feb 2005, *H. Kennedy & F. Ganders 5944* (UCR). **Mpio. Cozumel:** Isla Cozumel, 1 km NW del Faro de la Punta Celerain, 22 Nov 1985, *E. Cabrera et al. 9804* (MO). **Mpio. Felipe Carrillo Puerto:** 7 km E of Carrillo Puerto, 2 Nov 1984, *D. Neill et al. 5766* (MO). **Mpio. Lazaro Cardenas:** Yalahau Region, El Eden Reserve, ca. 30 mi NW of Cancún, 6 m, 26 Jun 2000, *G.P. Schultz et al. 1513* (MO, UCR), and about the same location 12 Jul 2000, *G.P. Schultz et al. 1530* (UCR). **Mpio. Othon P. Blanco:** 500 m S del Cenote en Bacalar, 15 May 1999, *R. Durán et al. 3271A* (MO). **Mpio. Solidaridad:** X'cacel a X'cacelito, ca. 13 km N de Tulum, 14

Jun 1998, *C. Gallardo et al. 2220* (MO). **Yucatan. Mpio. Chemax:** 3 km W de Chemax, 16 Jul 1985, *E. & H. Cabrera 8868* (MO). **Mpio. Conkal:** camino Conkal a Yaxkukul, 5 m, 4 Nov 1997, *F. Tun, J.A. González-Iturbe 335* (SEL). **Mpio. Halacho:** Rancho El Naranjo, 12 m, 8 Sep 1988, *L.M. Ortega T. & E. Mena P. 787* (UCR). **Mpio Maxcanú:** Chunchucmil, 5 km a la redonda, 11m, 4 Aug 1986, *C. Chan 6864* (CIQR). **Mpio. Muna:** km 10 carr. Muna a Opichén, 50 m, 24 Sep 1984, *C. Chan 3991* (UC). **Mpio Oxkutzcab:** zona arq. de Sayil, 25 Dec 1985, *E. & H, Cabrera 10368* (CIQR, MO). **Mpio. Tekax:** Tekax, 18 Nov 1992, *F. May 775* (CIQR). **Mpio. Tixcacalcupul:** S de Xchak Hua, 13 Nov 1991, *M. Méndez et al. 398* (MO). **Mpio. Tizimín:** 6 km W de Tizimín rumbo a Sucilá, 22 Sep 1996, *R. Durán et al. 2619* (MO). **Mpio. Tunkas:** carr. rumbo Quintana Roo pueblo, 23 m, 19 Jan 1982, *E. Ucan et al. 1840* (NO). **Mpio. Tzucacab:** hills above Tzucacab, 16 Feb 1983, *D.A. White 271* (NO, JBSD). **Mpio. Valladolid:** Xuilub, 22 m, 24 Jun 1989, *M.C. Sanchez 342* (UAGC). **Mpio. Yaxcaba:** Tixcacaltuyub, 24 m, 29 Sep 1981, *C. Vargas & P. Sima 540* (NO); S.E. Kancabconot [Kancabdzonot], [27 m], May 1917, G.F. Gaumer 23862 (C, MO).

4b. Diospyros yucatanensis Lundell subsp. **yucatanensis** (**Figs. 46, 47a–o, 48c–d**).

Trees or shrubs, 3–15(–28) m tall; **trunk** up to 45 cm in diameter; **stems** usually glabrous, vestiture sometimes persisting into the 2nd year, the young stems glabrate to densely orangish to reddish-brown tomentose or wavy-hairy, sometimes with some straight ascending hairs, clavate glandular hairs sometimes present, deciduous, leaving the dark reddish-brown epidermis viscid and shiny. **Petioles** (3.5–)4–6.5(–8) mm long, ± rugose, golden or reddish-brown to very dark brown, viscid or glaucous, densely ascending pubescent below, densely short wavy-hairy above. **Lamina** oblong ovate to oblanceolate, sometimes elliptic to obovate, rarely lanceolate, (65–)70–106(–117) mm long, (20–)25–41(–47) mm wide, the length to width ratio (1.8–)2.2–3(–3.4) **:** 1, lamina at 0.75 length usually 19–30 mm wide, yellow-green in life (Lundell 1937), *base* rounded to the petiole or abruptly short-decurrent on the petiole, *margins* slightly revolute, *apex* acuminate or acute, sometimes rounded; **lower lamina surface** densely bright orange-red to tawny tomentulose, the hairs sometimes deciduous, the hair bases often swollen, the epidermis reddish-brown to gray, the stomatal apparatus dense, usually opaque and conspicuous; **upper lamina surface** reddish wavy-hairy, the epidermis sometimes crystal-papillose. **Venation** brochidodromous to arcolanguid; **midrib** densely bright reddish-brown tomentulose, with some longer, straight, subappressed hairs; **lateral veins** mostly prominent below, often bright reddish-brown velutinous, flush to finely raised above; **3° veins** ± raised below and obscured by the vestiture, slightly impressed or obscure. **Male inflorescences** 1–5-flowered cymes, tomentulose to wavy-hairy, the epidermis viscid, dark brown; **peduncles** 2–5 mm long; **pedicels** 1–3 mm long, bracts linear lanceolate, 1–3 mm long. **Male flowering calyx** densely golden to reddish tomentulose to short wavy-hairy outside, with some longer hairs, *tube* (3–)4.5–5.5 mm long, 4.5–5.5 mm wide, the upper 1/2 sericeous, lower 1/2 glabrous, *lobes* oblong-ovate to triangular, 3.5 mm long, 2.8–3.5 mm wide, subacute to barely acuminate, sericeous inside with a somewhat narrow tomentulose intramarginal band; **male corolla tube** (6.5–)9–10 mm long, 3–4 mm wide, sericeous except for 3 shield-shaped glabrous basal regions, 0.5–1.5 mm long, and some very minute wavy hairs just distal to these; **male corolla lobes** oblong-ovate, 3–5 mm long, 1.5–2.3 mm wide, reddish to brownish sericeous outside. **Stamens** 12–14; **filaments** adnate ± at the base of the corolla, a few stamens sometimes inserted on the receptacle, sometimes geminate, (1.5–)2–3.5 mm long; **anthers** lanceolate to ovate or oblong-ovate, 3–4.5 mm long, sometimes rostrate or cuspidate, apex thickened or granular. **Female inflorescences** 1–3 mm long, bracts deciduous (not seen by us), reported by Lundell (1937) to be oblanceolate and 3mm long. **Female flowering calyx** densely hairy, *tube* 2.5 mm long, 5 mm wide, sericeous except near the base where glabrous, *lobes* subacute to obtuse, 6 mm long, 5.5 mm wide, slightly rounded or tapering to a blunt point, sericeous inside with a wide tomentulose intramarginal band; **corolla tube** 3 mm long, 2.5 mm wide, the upper 2/3 reddish sericeous outside, lower 1/3 with 3 overlapping shield-shaped glabrous regions; **corolla lobes** ovate, 4 mm long, 3 mm wide; **ovary** ovoid, reddish sericeous; **styles** 3, spreading; **stigmas** bifid; **staminodes** 3, adnate to the corolla tube near the base, anther-like. **Fruiting pedicels** 2–6(–8) mm long, densely hairy. **Fruiting calyx tube** (3–)3.5–5.5(–7) mm long, sericeous except near the base, *lobes* widely oblong, 3–6(–8) mm long, (7–)9–12(–13) mm wide, rounded or obtusely tapered to a blunt point, spreading, sericeous except near the base, the hairs of the intramarginal band sparser than in the flowering calyx; epidermis puncticulate. **Fruit** globose, immature fruit sparsely tawny to reddish-brown hairy, mature fruit ± glabrous, but densely hairy near the apex.

The two collections Lundell used to describe male flowers were based on collections from Yucatan by Gaumer; one from Kancabdzonot, the other without a specific locality. The specimen from Kancabdzonot is representative of *D. y.* subsp. *spectabilis*, while the collection lacking a precise locality is inadequate for determination to the subspecific level. The nominate subspecies of *D. yucatanensis* has a more southern distribution than *D. y.* subsp. *spectabilis* (Fig. 49). It occurs in the eastern extreme of coastal Veracruz, Tabasco, parts of Campeche, the northern highlands of Chiapas, Mexico, the mountainous parts of Belize, and through a large part of northern Guatemala. We have seen three collections that are biogeographically difficult to explain at this time, two from northern Quintana Roo, including one from the southern part of Cozumel, and another from near Popolna, and a collection from near Sayil in the state of Yucatan. It grows on thin or rocky soils in evergreen forest, deciduous forests, and secondary forest derived from these vegetation types, usually between sea level and 360 m, but at elevations up to 700 m in Belize, and 1400 m in Chiapas, Mexico. It is sometimes associated with cliffs. The distribution of this taxon apparently overlaps with both *D. acapulcensis* subsp. *veraecrucis* and *D. a.* subsp. *acapulcensis* in northwest Chiapas. We have seen single collections of hybrid material between *D. yucatanensis* and each of these subspecies from this region.

Representative specimens. **BELIZE. Cayo:** brecha al W del "Rancho Indio Suizo," 8 mar 1985, *E. Cabrera et al. 7719* (CIQR). **Toledo:** ca. 6.5 mi W of Medina Bank, 800–1200 ft, 23–27 Apr 1976, *G.R. Proctor 35991* (MO); Mountain Pine Ridge, San Agustin, Jul–Aug 1936, *C.L. Lundell 6807* (ARIZ). **GUATEMALA. Baja Verapaz:** El Mago, 26 Oct 1968, *E. Contreras 8015* (XAL, F). **Izabal:** Bay of Santo Tomás, 0–2 m, 13 Apr 1940, *J.A. Steyermark 39366* (F); Puerto Mendez, bordering Sarstun River, 5 km, 9 Oct 1969, *E. Contreras 9293* (MO); Río Dulce, N side, between Livingston and 6 mi up river, 1–25 m, 14 Apr 1940, *J.A. Steyermark 39427* (F). **Peten:** Lake Petén, 3 May 1933, *C.L. Lundell 3194* (F); Umgebung des Westufers des Lago Peten Itza, La Providencia" (= "La Trinidad"), 170 m, 17 Aug 1993, *B. Wallnöfer & F.M. Tut-Tesucun 5941* (MO); San Miguel, 14 Dec 1967, *E. Contreras 7316* (F, IJ); Tikal N.P., top of Temple Two, 8 Jul 1959, *C.L. Lundell 16257* (IJ, F). **MEXICO. Campeche. Mpio. Carmen:** cerca de la Est. del Carmen, del ICMyL, UNAM, ca. 9 km E de Cd. Carmen, 23 Nov 1987, *E. & H. Cabrera 14830* (MO, IEB); Colonia Nueva Coahuila, 10 m, 15 Jan 1982, *C. Chan 1118* (XAL). **Chiapas. Mpio. Las Margaritas:** W side of Laguna Miramar, 350 m, 11 Feb 1973, *D.E. Breedlove 33386* (CHAPA). **Mpio. Ocosingo:** 7 km E de El Carmen Pataté, 900 m, 10 Apr 1991, *E. Martínez S., C.H. Ramos & C. Eufrosio 24581* (XAL). **Mpio. Ocozocoautla:** Res. del Ocote, 380 m, 6 May 1983, *J.I. Calzada 10003* (XAL). **Mpio. Palenque:** La Montaña, desviación a Sn. Juan Bautista, 20 m, 5 Jul 1999, *C. Gutiérrez B. & J. Balam 6607* (UCAM). **Mpio. San Fernando:** between San Fernando and Moravillas, 840–940 m, 15 Feb 1987, *T.B. Croat & D.P. Hannon 65041* (MO). **Quintana Roo. Mpio. Cozumel:** parte S de la isla, 4 m, 27 Aug 1985, *C. Chan 5619* (CIQR). **Mpio. Lazaro Cardenas:** 2 km E de Popolna, 12 Nov 1980, *E. Cabrera & L. Cortez 256* (MO, CIQR). **Mpio. Solidaridad:** 12 km S del Ejido Laguna OM, 7 Aug 1980, *O. Téllez & E. Cabrera 3058* (MO). **Tabasco. Mpio. Balancan:** Balancan, 9 Dec 1975, *A. Novelo et al. 186* (K, MO, ARIZ, XAL); San Isidro, 7–11 Jun 1939, *E. Matuda 3378* (K, NA, CAS, MO). **Mpio. Emiliano Zapata:** 9 km SE de Emiliano Zapata, 20 Nov 1986, *E. & H. Cabrera 12471* (MO). **Mpio. Huimanguillo:** Cuauhtemotzín, 0 m, 2 Dec 1983, *F. Ventura A. 20848* (MO, XAL, IEB). **Mpio Tenosique:** Tenosique, 14–16 Jun 1939, *E. Matuda 3401* (K, NA, MO, CAS). **Veracruz. Mpio. Pajapan:** Laguna del Ostión, 0–5 m, 28 Mar 1980, *L. Gutierrez 91* (XALU). **Yucatan. Mpio. Oxkutzcab:** 4 km W de Sayil, 20 m, 25 Oct 1984, *A. Espejo et al. 1235* (CHAPA).

Diospyros yucatanensis Lundell var. **longipedicellata** Lundell, Contr. Univ. Michigan Herb. 7:45. 1942.

Type: MEXICO. Yucatan: Chichen Itzá off Kaua road in advanced deciduous forest [as on label], "along Kaua road, east of Chichen Itzá, in advanced deciduous forest" [protologue], [20°40'W, 88°33'N, 29 m], Jun 11 [protologue], Jun–Jul [specimen], 1938, *C.L. Lundell & Amelia A. Lundell 7509* (holotype: MICH; isotypes: WTU!, LL, digital image!).

Lundell described this taxon based on its long male flowering pedicels. The small amount of material we have seen shows similarities in leaf and inflorescence characters to both subspecies, while the male flowering peduncles (e.g., *C. Chan 5110*) seem rather long for each subspecies. We suspect this name is synonymous with *D. y.* subsp. *spectabilis*, but would like to see material with fruit from Chichen Itzá before taking a position on the status of this taxon.

Additional material examined: **Mpio. Izamal:** K'axek, rumbo a Tunkas, 20 m, 17 Apr 1985, *E. Ucan et al. 3812* (CIQR). **Mpio. Tinum:** Tinum, alrededor del cenote Xholak, en Chichen Itzá, 25 m, 25 May 1985, *C. Chan 5110* (CIQR); Chichen Itzá, in second growth, *C.L. Lundell & A.A. Lundell 7434* (CAS, WIS).

MULTIVARIATE ANALYSES RESULTS AND DISCUSSION

A total of 23 leaf and fruiting inflorescence characters were used in the analyses (Table 1). From these, four character subsets were derived from the matrix, with lamina length and lamina width treated as priority characters, and $R < 0.7$ and $R < 0.8$ used as exclusion values (Table 2). A summary of the resulting biplots

TABLE 2. Subsets of characters used in principal component analyses.

Subset 1. Lamina length priority, R < 0.7	**Subset 3. Lamina width priority, R < 0.7**
lamina length	lamina width
lamina length : lamina width	lamina length : lamina width
lamina width at 0.75	petiole length
lamina width at 0.25 : lamina width	lamina width at 0.25 : lamina width
lamina width at 0.75 : lamina width	lamina width at 0.75 : lamina width
lamina length : distance between four centermost veins	lamina length : distance between four centermost veins
pedicel length	pedicel length
sepal width	sepal width
sepal length	sepal length
calyx tube length	calyx tube length
Subset 2. Lamina length priority, R < 0.8	**Subset 4. Lamina width priority, R < 0.8**
lamina length	lamina width
lamina length : lamina width	lamina length : lamina width
petiole length	petiole length
lamina width at 0.25	lamina length : lamina width at 0.25
lamina width at 0.75	lamina width at 0.25 : lamina width at 0.75
lamina length : lamina width at 0.25	lamina width at 0.25 : lamina width
lamina width at 0.25 : lamina width at 0.75	lamina width at 0.75 : lamina width
lamina width at 0.25 : lamina width	lamina length : distance between four centermost veins
lamina width at 0.75 : lamina width	pedicel length
lamina length : distance between four centermost veins	sepal width
pedicel length	sepal length
sepal width	calyx tube length
sepal length	sepal width : calyx tube length
calyx tube length	
sepal width : calyx tube length	

for PCA of the subsets is provided in Table 3. A biplot for subset 2 (leaf length given priority, R < 0.8) is presented for demonstration purposes (Fig. 50). Overall, biplots supported the four species groups identified by conventional taxonomic methods. In biplots of PC1 vs. PC2, *Diospyros acapulcensis*, *D. yucatanensis* and *D. aequoris* each tended to form distinct clusters that overlapped to varying degrees in the area where the PC-axes converged. *Diospyros salicifolia* collections typically formed a subcluster in this region of overlap. *Diospyros intricata* formed a cluster most closely associated with *D. aequoris*, but effectively separated from other taxa along the PC2-axis. The putative interspecific hybrid usually grouped with collections of *D. acapulcensis*. Separation of the taxa into groups along the PC3-axis was usually poor, although *D. intricata* separated completely from the other taxa in subset 4.

The intermediate position of *D. salicifolia* in the biplots suggests a hybrid origin for *D. salicifolia*. If this is the case, then based on geography, the likely parent taxa are *D. aequoris*, perhaps a form similar to subsp. *chutlensis* of western Guerrero, and the nominate subspecies of *D. acapulcensis*. However, we have no direct evidence that hybridization occurs between these taxa. Inflorescence size characters are clearly more similar to *D. aequoris* subsp. *chutlensis* than the nominate form of *D. acapulcensis*. However, leaf characters of *D. salicifolia*, such as lamina size, shape, and venation, usually group clearly with one putative parent or the other, and often represent the extreme measurements for that character among the three taxa. In general, specimens of *D. salicifolia* are rather consistent with respect to qualitative and quantitative characters. At any rate, it seems most unlikely that specimens of *D. salicifolia* represent F1 hybrids of the possible parent taxa, since neither of these species occurs with *D. salicifolia*, nor are the parent taxa currently believed to be

TABLE 3. Summary of biplots resulting from PCA of subsets 1–4.

	Axes	Separation
Subset 1.		
	PC1	*D. acapulcensis* is separated from *D. yucatanensis* and *D. aequoris* with minor overlap.
	PC2	*D. intricata* is separated from all other taxa. *D. aequoris* is separated from *D. yucatanensis* with slight overlap, and is tending to separate from *D. acapulcensis*.
Subset 2.	PC1	*D. yucatanensis* is nearly completely separated from *D. acapulcensis*. *Diospyros aequoris* is separated from *D. acapulcensis* with small amounts of overlap.
	PC2	*D. aequoris* is separated from *D. acapulcensis* with small amounts of overlap, and separated from *D. yucatanensis* with minor overlap. *D. intricata* is effectively separated from all other taxa.
Subset 3.		
	PC1	*D. acapulcensis* and *D. yucatanensis* are separated with minor overlap.
	PC2	*D. aequoris* is separated from *D. yucatanensis* and *D. acapulcensis*, but with some overlap. *D. intricata* is effectively separated from all other taxa.
Subset 4.		
	PC1	*D. acapulcensis* and *D. yucatanensis* are nearly completely separated.
	PC2	*D. aequoris* separates from *D. yucatanensis*, but with some overlap, and tends to separate from *D. acapulcensis*, but with considerable overlap.
	PC3	*D. intricata* separates completely from other taxa.

sympatric anywhere. The possibility of a recent hybrid origin for *D. salicifolia* could not be addressed sufficiently by the current study. It would be worthwhile to pursue genetic evidence for or against this hypothesis using DNA microsatellite markers, ex situ cross-fertilization experiments, or by looking for possible differences in chromosome number.

The *D. intricata* cluster was most associated with the *D. aequoris* cluster. *Diospyros intricata* is generally thought to be endemic to the Cape Region of Baja California Sur and Isla Cerralvo in the Gulf of California (We have not yet been able to verify material recently reported from an isolated upland locality on Isla Tiburón [Wilder et al. 2008]). Consequently, it is separated from all other taxa of the *salicifolia* complex by the Sea of Cortez. The range of *D. intricata* is more closely approached by *D. aequoris* (in Sinaloa) than *D. acapulcensis* (in Jalisco). We have not seen any collections that appear to be intermediate between *D. aequoris* and *D. intricata*.

The characters with the highest loadings for the rotated principal components (RPC) are reported in Table 4. High loadings in the rotated factor patterns were most often seen in inflorescence size variables, although leaf size characters had the highest loadings for subset 2. While inflorescences size characters proved useful in explaining the variation in the data set, they were not much used during conventional taxon delimitation (perhaps some in the case of *D. yucatanensis*). Leaf size and shape characters were useful in explaining variation in the data as well, while inflorescence shape characters were relatively less important. Conversely, some characters that were important during conventional taxon delimitation (i.e., hair base morphology, leaf thickness, prominence of venation, etc.) were not considered during PCA. It should be remembered that interpretation of the rotated factor patterns does have a subjective element. Still, it appears significant that PCA found groups consistent with those found during conventional taxonomic procedures, even though the RPC highlighted a somewhat different set of characters. It thus provides a somewhat independent confirmation of the existence of the identified groups.

ACKNOWLEDGMENTS

We would like to express our appreciation to UCMEXUS and the UCR Center for Conservation Biology, CIIDIR-IPN, Jiquilpan, Michoacan, and Dr. Giles Waines (UCR), for their support of taxonomic work on Mesoamerican persimmons. We would also like to thank Paulo T. Sano and an anonymous reviewer for their many useful comments on the manuscript. Access to microscopes was kindly made possible by Martha L. Orozco-Cardenas at the UCR Plant Transformation Research Center. We thank Guy Nesom for

TABLE 4. Characters with highest loadings for RPC of subsets 1–4.

	RPC 1	RPC2	RPC3	RPC4	RPC5
Subset 1.					
	pdL	LL	SW	LL:LW	
	SL	LW3/4	CL		
Subset 2.					
	LL	LW1/4:LW3/4	pdL	LL:LW1/4	SW
	ptL	LW1/4:LW	SL		CL
	LW1/4	LW3/4:LW	SW:CL		
	LW3/4				
Subset 3.					
	pdL	SW	LW	LL:LW	
	SL	CL	ptL	LL:V	
Subset 4.					
	pdL	LW1/4:LW3/4	LL:LW	SW	LW
	SL	LW1/4:LW	LL:LW1/4	CL	ptL
	SW:CL	LW3/4:LW			

providing Latin diagnoses, Ed Plummer for technical support, Jose Aguilar Patiño (UAS), Francisco Santana-Michel (ZEA), Antonio Machuca (CREG), Teresa B. Salvato (UCR), C. Conrado, Jeffrey Ross-Ibarra, and Randy Richmeier for field assistance. We are grateful to Jeffrey Ross-Ibarra for his assistance with the statistical investigations. Much appreciated specimen loans and images were provided by: AAU, ARIZ, B, BH, BM, BRH, C, CAS, CHAPA, CIIDIR, CIMI, CIQR, DES, E, EBUM, F, FLAS, FR, GB, HUAA, IEB, IJ, ILL, JBSD, K, LSU, MAD, MSCH, MO, MOU, NA, NLU, NO, P, SD, SEL, TEFH, TEX, UAGC, UC, UCAM, UCR, UCSB, UMO, US, USF, UTEP, XAL, XALU, VT, WIS, WTU, ZEA.

APPENDIX 1

Representative subspecific intermediates and interspecific hybrid specimens:

Diospyros acapulcensis subsp. **guanacastensis** interm. with **D. acapulcensis** subsp. **rivensis. COSTA RICA. GUANACASTE:** Cerro El Hacha, P.N. Guanacaste, 1100 m, 15 Sep 1991, *R.E. Espinoza 120* (MO, BM). **SAN JOSÉ:** Río Uruca, near Santa Ana, 900 m, 7 Jan 1970, *W.C. Burger & R.L. Liesner 7180* (MO). **PUNTARENAS:** Nicoya Peninsula, Curú, 2–75 m, 31 Aug 1995, *A.C. Sanders et al. 17728* (UCR); Cantón de Acosta, San Ignacio, Río Candelaria, 700 m, 10 Aug 1993, *J.F. Morales 1576* (MO).

Diospyros acapulcensis subsp. **rivensis** interm. with **D. acapulcensis** subsp. **nicaraguensis. NICARAGUA. LEON:** Sector NE de la Isla de Momotombito, 200 m, 21 Oct 1979, *M. Araquistain 371* (MO); Sector W de la Isla Momotombito, 150–200 m, 27 Jan 1980, *M, Araquistain & P. Moreno 1061* (MO). **MANAGUA:** Campus of Escuela Americana, 200 m, 20 Oct 1976, *D. Neill 1088* (MO).

Diospyros acapulcensis subsp. **pedromorenoi** interm. with subsp. **nicaraguensis. CHONTALES:** Hacienda Corpus, ca. 100 m, 5 Sep 1982, *W.D. Stevens 21802* (MO); **ESTELÍ:** Llano El Pozo, 18 km E de Estelí, 1260–1300 m, 23 May 1983, *P. Moreno 21380* (MO). **LEON:** Volcán Momotombo, 200 m, 29 Jan 1980, *M. Araquistain & P. Moreno 1082* (MO). **MATAGALPA:** Valle "Pueblo Viejo," 500 m, 2 Feb 1984, *P. Moreno 22958* (MO).

Diospyros acapulcensis subsp. **rivensis** interm. with **D. acapulcensis** subsp. **veraecrucis. HONDURAS. VALLE:** Amapala, Isla de la Tigre, falda W del cerro volcanico, 0–400 m, 4 Apr 1981, *C. Nelson & H. Martínez C. 7743* (MO, TEFH);

Diospyros aequoris subsp. **balsensis** interm. with subsp. **martineziana. MÉXICO. MICHOACAN:** Mpio. Huetamo: a 8 km al NW de San Jeronimo, carretera Huetamo-Churumuco, 370 m, 20 Mar 1981, *J.C. Soto N. et al. 2687* (MO, XAL, ILL).

Diospyros aequoris subsp. **rekoi** interm. with subsp. **tehuantepecensis. MEXICO. OAXACA:** Mpio. Salinas Cruz: El Coyol, 2 km al W de Salina Cruz, 17 Mar 1981, *T.P. Ramamoorthy et al. 2014* (IEB); Mpio. Santiago Astata: Playa La Colorada, 1.8 km al W, 40 m, 30 Jul 2000, *Silvia Salas M. 3163* (IEB); Mpio. Tehuantepec: Cerro Lieza, 2 km NW de Tehuantepec, 1 Nov 1996, *Cipriano Martínes R. 757* (MO).

Diospyros yucatanensis subsp. **spectabilis** interm. **Diospyros yucatanensis** subsp. **yucatanensis. GUATEMALA. PETEN:** Río Pasion, Laguna San Juan Acul, 11 Feb 1964, *C.L. Lundell 17946* (F). **MEXICO. CAMPECHE:** Mpio. Candelaria: entre Candelaria y Venustiano Carranza, 9 Aug 1996, *P. Zamora C. & D. Méndez D. 5348* (UCAM); Mpio. Escársega: 5 km al N de Escársega, 8 m, 16 Nov 2003, *C. Gutiérrez B. 8036* (UCAM); Mpio. Hopelchén: Xcochkax, 30 m, 9 Mar 1987, *J.N. Labat 1918* (IEB).

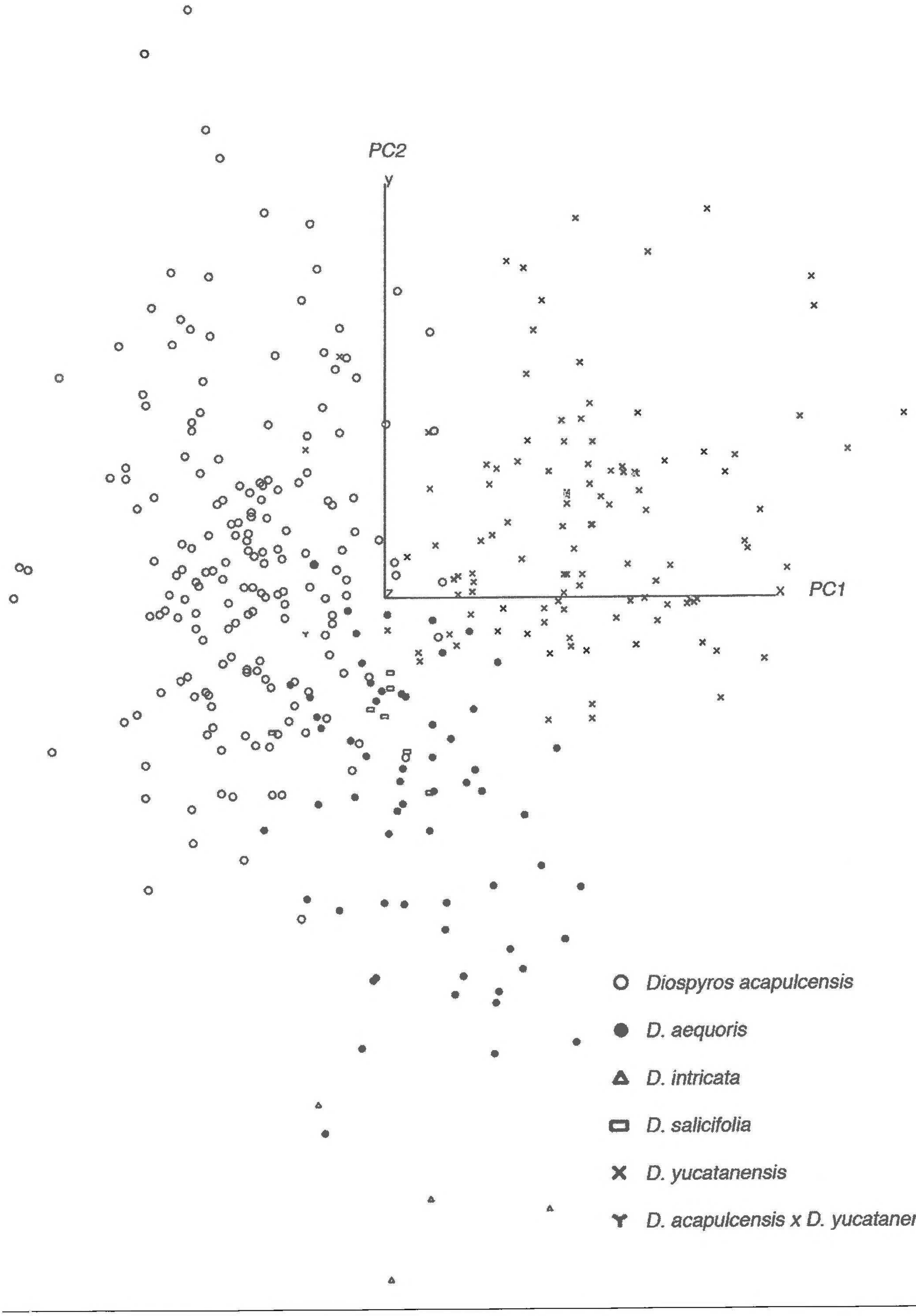

Fig. 50. Biplot of PC1 vs. PC2 for subset 2 (leaf length given priority, R < 0.8).

Diospyros yucatanensis subsp. **yucatanensis × D. acapulcensis** subsp. **acapulcensis. Mpio. Chiapa de Corzo:** Río Grijalva, 10 km W of Chiapa de Corzo, 500 m, 16 May 1972, *D.E. Breedlove 25167* (MO).

Diospyros yucatanensis subsp. **yucatanensis × D. acapulcensis** subsp. **veraecrucis. MEXICO. Chiapas:** Mpio. Ocozocoautla de Espinosa: 3 km N of Ocozocoautla along road to Mal Paso, 1 Feb 1973, *D.E. Breedlove 32870* (CHAPA).

Diospyros yucatanensis subsp. **yucatanensis × D. acapulcensis** subsp. **nicaraguensis. GUATEMALA. Baja Verapaz:** Opp. El Rancho, 2300 ft, 12 Jan 1908, *W.A. Kellerman 7990* (F), and same location, 2500 ft, 5 Jan 1908, *W.A. Kellerman 7640* (F [2 sheets]).

APPENDIX 2

Specimens examined of ***Diospyros* aff. *inconstans*: PANAMA. Darien:** El Real, 1–3 km S. of town, near sea level, 7 Jan 1975, *A. Gentry 13458* (MO, TEFH); El Real, 1 Mar 1972, *A. Gentry 4508* (MO); Río Tuira, vicinity of El Real, 14 Jun 1959, *W.L. Stern et al. 455* (MO); same location, 1 Jul 1959, *W.L. Stern et al. 763* (MO); El Real, near airport, 13 Jul 1971, *T.B. Croat & Porter 15467* (TEFH); El Real, Quebrada Trapiche, [without date], *J.A. Duke & N. Bristan 324* (MO).

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